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Seasonal Distribution and Abundance of Tidepool Fishes at Six Locations within the Southern California Bight, 2004-2005

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Abstract.—Several studies have been conducted on the California coast investigating the distribution and abundance patterns of rocky intertidal fishes; however, most of these studies have focused on only one or two sites along a large expanse of coastline primarily north of Point Conception. This study examined six sites in the central portion of the Southern California Bight to assess regional patterns of abundance and distribution of rocky intertidal fishes more accurately. All six sites were sampled within the same low tide series quarterly from January 2004 to February 2005. Species abundances, biomass, densities, species diversity (H′), and size distributions were determined and compared. All assemblages were dominated by *Clinocottus analis* (Cottidae) both in abundance and biomass although a total of ten species were found throughout the study representing six families. Species composition did vary with latitude as warm temperate species, *Girella nigricans* and *Gobiesox rhessodon*, were associated with southern sites, and cool temperate species, *Clinocottus recalvus* and *Oligocottus snyderi*, were found at northern sites. Differences in community structure may reflect site specific environmental conditions such as surfgrass coverage or wave energy. When considering abundance and density, each metric yielded a different result, i.e., the site with greatest abundance had the lowest density. This may be reflective of a funneling effect of intertidal fishes from surface area of habitat available at high tide to low tide rather than simply standardizing for pool size. H′ was not influenced by season or latitude but was negatively correlated with wave exposure. Three of the five most common species (*Clinocottus analis*, *Girella nigricans* and *Gobiesox rhessodon*) recruited in the late fall, early winter. Assessment of *Clinocottus analis* by site revealed regional variation: recruitment was only detected at the three southern sites in January 2004 but at all six sites in February 2005.

Southern California rocky shores differ from those in central and northern California in both community structure and oceanographic influences. In the rocky intertidal zone, the algal community north of Point Conception is primarily dominated by brown algae and large foliose red algae as opposed to more turf-forming species south of Point Conception (Murray and Bray 1993); thus, biomass of algal species greatly decreases in the southern California rocky intertidal (Murray and Bray 1993). While differences in rocky intertidal fish assemblages also likely exist between the northern and southern coasts, little is known about the community structure of fishes in the Southern California Bight. These fishes have remained largely overlooked primarily because their cryptic nature and

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ability to move make them difficult to sample. The coastline within the bight receives less northwesterly wind and wave energy than that to the north due to south facing shores in many areas and protection from the Channel Islands (Hickey 1993). Also, sea surface temperatures generally are warmer and sandy beaches are more prevalent in the south than on the central and northern coast. Is this change in both oceanographic influence and algal species composition accompanied by a change in the community structure of rocky intertidal fishes?

The Southern California Bight, extending from Point Conception to the Mexico border, provides a unique mix of warm-temperate and cool-temperate subtidal fish species influenced by the eddying effect of the California Current (Hickey 1993; Horn et al. 2006). Within the Bight cool waters from the north mix with warm waters from the south resulting in a transition zone between northern and southern fishes. Nearshore fishes associated with warm water generally are found in greater abundance to the south and those associated with cooler water are found primarily to the north. Also, localized temperature regimes and habitat play an important role in dictating species composition. While this same pattern may be true of intertidal fish species in general, few studies have assessed the distribution of intertidal fishes in the Southern California Bight (Crase 1992; Davis 2000; Craig and Pondella 2006).

Several studies have examined the abundance and distribution of rocky intertidal fishes on the California coast north of Point Conception (Graham 1970; Burgess 1978; Grossman 1982; Yoshiyama 1981; Yoshiyama et al. 1986; Shanks and Pfister 2009). Given that Point Conception is a known biogeographic barrier between northern and southern nearshore fish species (Horn and Allen 1978; Allen 1985; Horn et al. 2006) and that such a defined difference exists in oceanographic processes and intertidal community structure, it is surprising that rocky intertidal fish assemblages south of Point Conception remained largely overlooked until the mid-1990's (Crase 1992; Davis 2000, Craig and Pondella 2006).

Prochazka et al. (1999) summarized the biogeography of intertidal fishes found along the eastern Pacific coast. They divided the region into three subregions based on intertidal fish faunas: the first extended from Alaska south to Point Conception, the second from Point Conception to Ecuador, and the third extended along the South American coast. They described the first region as low in species richness (average of 15 species per site) compared to Indo-West Pacific assemblages and the second region as high in species richness with an average of 25 species per site. While the authors conceded that a lack of coverage of studies may impact the results of their assessment (only one southern California study was included in the second region (Cross 1982), their conclusions paint an inaccurate picture of southern California intertidal fish assemblages, i.e., one of high species richness.

Localized assessments of distribution and abundance of intertidal fishes in California (Horn and Martin 2006) reveal differences in familial dominance and in species richness between northern, central and southern California. The Cottidae (sculpins) dominate northern and southern assemblages, but the Stichaeidae and Pholidae comprise the greatest percentage of total catch in central California, and the Clinidae dominate northern Baja California. Species richness is greatest at northern sites (18 species) and central sites (17 species), and lowest in southern California (seven species). The authors suggest this may reflect the overall dominance of intertidal fish assemblages by cold-temperate species.

Patterns of species richness and familial associations identified along the California coast (Horn and Martin 2006) persist over varying temporal scales. Numerous studies conducted over periods less than three years (Grossman 1982; Stepien et al. 1991; Crase 1992; Gibson

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and Yoshiyama 1999) demonstrate predictability of intertidal ichthyofaunal assemblages, minus significant environmental perturbations such as an El Niño Southern Oscillation (ENSO) event (Davis 2000). Even comparisons of species composition and abundance over greater time scales of five years or more indicate consistency (Yoshiyama et al. 1986; Horn and Martin 2006) of dominant families and species though not necessarily abundances. Any changes detected likely are attributable to variability in spawning and recruitment success due to dynamic environmental conditions (Thomson and Lehner 1976; Gibson and Yoshiyama 1999; Davis and Levin 2002).

While a growing number of studies indicate intertidal fish spawning and recruitment can be impacted by changes in environmental conditions, it is not known how community structure might respond to climate change. With increasing sea surface temperatures, some species may exhibit northward shifts in abundance following their optimal thermal regime (Sagarin et al. 1999; Horn and Martin 2006), some might adapt to new environmental conditions, and still others may become extinct. Repeated sampling of intertidal fish assemblages has provided valuable information regarding temporal and spatial variation. Without continued sampling, any changes or shifts in distribution and abundance that would accompany increasing temperatures might go unnoticed. Additionally, shifts may occur on a small spatial scale thus current coastal coverage may provide inadequate baseline data with which to detect change.

Many aspects of the ecology, physiology, and distribution of intertidal fishes have been investigated (Thomson and Lehner 1976; Barton 1982; Grossman 1982; Davis 2000; White and Brown 2013; Richards 2011; Shanks and Pfister 2009; Martin 2014; Mandic et al. 2014; Knope et al. 2017; Rangel and Johnson 2019) including community structure, but all of these studies were limited to one or two sites in very close proximity. Yoshiyama et al. (1986) reviewed studies of intertidal fish assemblages in California from Cape Arago to Piedras Blancas, but similar numbers and coverage of studies do not exist for southern California. Therefore, to better understand rocky intertidal fish assemblages and how they vary over time and space, the current study was designed to cover multiple sites over an expanse of coastline in southern California.

The present study describes tidepool fish assemblages at six sites covering 150 km in the central portion of the Southern California Bight with all sites sampled in the same low tide series for each sampling period. Additional goals of this study were to: 1) compare variation in fish assemblages by latitude, season, and wave exposure, 2) identify associations between fish species and environmental variables, and 3) detect recruitment pulses for individual species.

Materials and Methods

The study area extended approximately 150 km along the coastline of the Southern California Bight from northern Los Angeles County to Orange County (Fig. 1). Sites were sampled quarterly for a period of 14 months (January 2004 to February 2005) with one overlapping season totaling five sampling seasons. Tidal heights in this area range from –0.6 to 2.1 m and low tides are semi-diurnal. Because of the timing of seasonal low tides, afternoon and evening tides were sampled during fall and winter while early morning tides were sampled during spring and summer. To eliminate variation among low tide series, all sites were sampled on days within the same series.

Six sites were selected based on distribution within the Bight and the number of discrete tidepools available within rocky benches. From north to south, sites were located at

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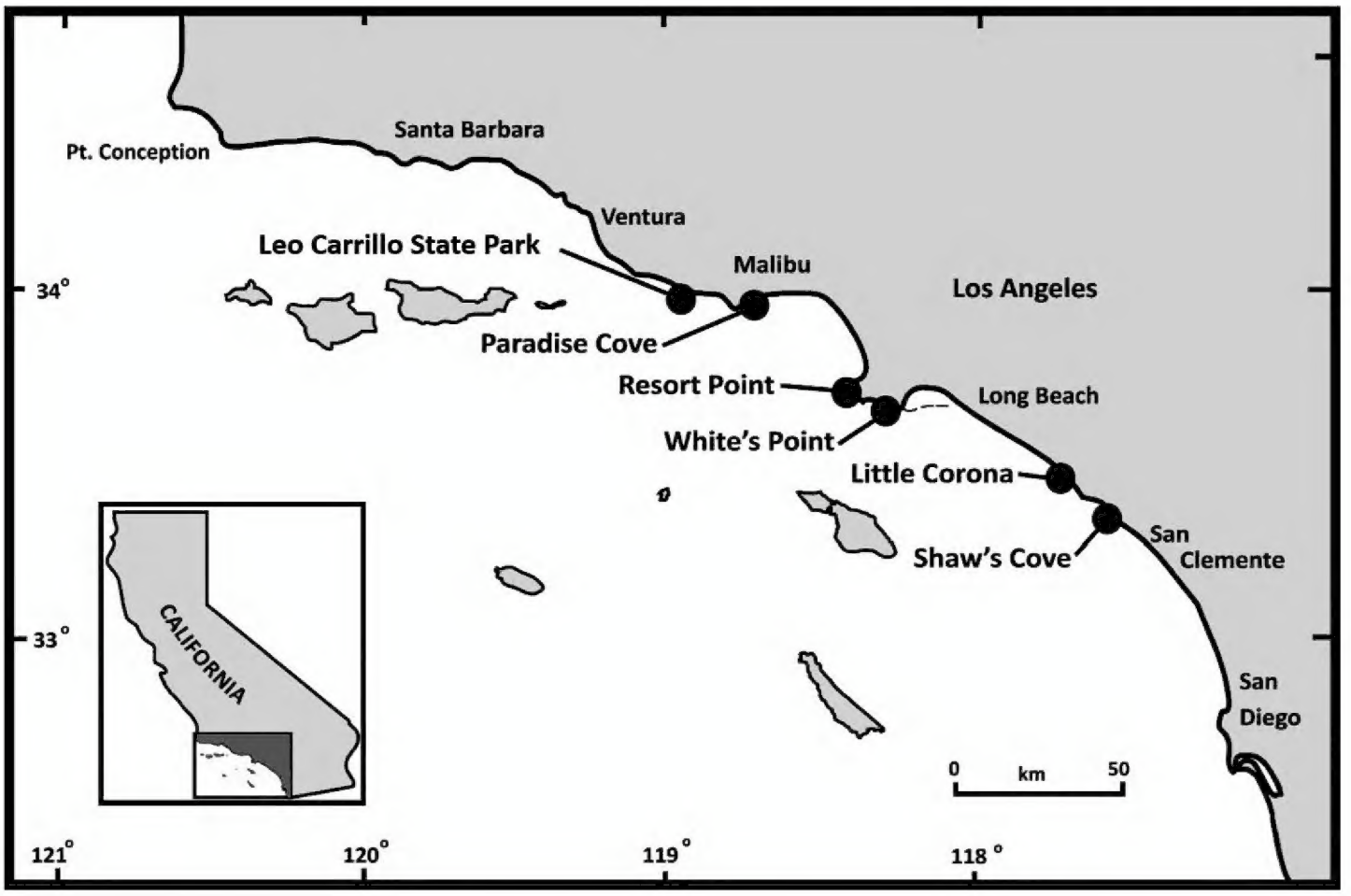

Fig. 1. Location of study sites within the Southern California Bight. Sites extended from Malibu, CA south to Laguna Beach, CA a distance of approximately 150 km.

Leo Carrillo State Park, Malibu (N 34.0431, W 118.9370); Paradise Cove, Malibu (N 34.0120, W 118.7921); Resort Point, Palos Verdes (N 33.7662, W 118.4244); White's Point, San Pedro (N 33.7141, W 118.3163); Little Corona, Corona del Mar (N 33.5891, W 117.8685); and Shaw's Cove, Laguna Beach (N 33.5450, W 117.7993) (Fig. 1). Pools were selected based on the following criteria: 1) complete separation from the ocean, 2) stability through time, 3) ability to make a complete search, and 4) size. Because all sites had to be sampled in the same low tide series, the number of pools at each site (Leo Carrillo, $n = 5$; Paradise Cove, $n = 5$; Resort Point, $n = 5$; White's Point, $n = 4$; Little Corona, $n = 4$; Shaw's Cove, $n = 5$) was dictated by how many could be sampled in one low tide period.

For the purposes of this study, we determined that a capture and release method involving draining and collecting would reduce impacts of the collection process. The same set of pools was sampled with replacement for each successive date of collection. Water was removed from each pool using a gas-powered, centrifugal pump with a mesh covered intake hose or bailed by bucket. The area of the pool was searched thoroughly with fish being collected by hand or dipnet. If no fish were found after a five-minute period, searching ceased. Boulders were moved and over-turned as necessary. Fish were placed in buckets with fresh seawater then identified, individually measured (standard length) to the nearest millimeter and weighed as a species group (wet weight via Pesola spring scales) to the nearest 0.5 gram. Boulders and cobble that were removed to adequately search for fishes were returned to original locations. Pools then were refilled, rocks were replaced, and fishes were returned to the pool from which they were collected.

Before each pool was drained, temperature (electronic thermometer), salinity (refractometer), pH (pH meter), and dissolved oxygen concentrations (DO meter) were measured

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for all sampling dates. Also, sea urchins and sea stars were counted, mussels and anemones were quantified (none, single, few, some, many), and percent cover of boulders, upright macroalgae, surfgrass, cobble/shell hash, and sand were visually estimated. Due to availability of the instruments, dissolved oxygen and pH were measured for only three of the five sampling dates, January 2004, May 2004, and December 2004. July 2004 dissolved oxygen was measured, but not pH. Neither dissolved oxygen nor pH were measured February 2004. Surface area and volume were measured for each pool. Surface area was determined by drawing the perimeter of each pool on graph paper and scaling each square to a representative unit of length. Each drawing was scanned into a digital image file. ImageJ (NIH) software was then used to measure the surface area for each pool by taking the mean of three freehand selections. Ten random depth measurements were taken throughout each pool. Volume was estimated by multiplying surface area by mean pool depth. These physical characteristics of pools were measured once. Effects of erosion rates on volume and surface area for the duration of this one-year study were negligible (Emery 1946). While sand levels did vary in a few pools at Shaw's and Paradise Coves, variation was slight and considered less than the error of the measuring technique.

Tidal heights were measured once for each pool using standard surveying equipment. A scope was placed on a level tripod at least a few feet above the highest pool. The bottom end of a stadia rod was placed at the surface of a pool and a relative height measurement was taken from the scope. At the precise time of predicted low tide, a measurement was taken of ocean surface level by this same means to calculate the tidal height of the scope and thus the tidal height of each pool.

Sites also were categorized by wave exposure. While many coastal regions can be categorized by qualitative assessment, southern California rocky intertidal areas experience seemingly more consistent exposure. We used a model-based approach that predicted site-specific relative exposures using predicted inshore wave height generated from the Coastal Data Information Program by the Scripps Institution of Oceanography (cdip.ucsd.edu). Waves are measured by two types of instruments. Pressure sensors measured the height of the water column passing over them from fixed underwater locations. Buoys rode atop the sea surface and measured their own acceleration as they rose and fell with each passing wave crest and trough. Both types of data generate sea surface elevations. The predicted inshore wave height model uses two wave models. The first, called Wavewatch III, is a wind-wave generation and propagation model. The second is a spectral refraction-diffraction wave model for shallow water (10 m > depth > 300 m) which models the effects of bathymetry on waves as they travel from deep water to the coast. The model used to specifically predict inshore wave heights combines these two models to predict wave heights at 10 m depth. While the model does not predict breaking wave height, it does provide a general measure of how much wave energy is reaching a particular area on the coast relative to other locations. To ground-truth the outcome of the model, two factors were considered at each site. Presence or absence of *Silvetia compressa* was noted as this algal species is associated with areas protected from wave action (Murray and Bray 1993). Also, tidal heights of vertical zones of algae and sessile invertebrates tend to increase at wave-exposed sites (Murray and Bray 1993) due to higher spray and wave run-up. Thus, tidal heights of pools where fishes were found likely would increase as well.

One site, Resort Point, required sampling over two days during the January 2003 sampling period. Pools 1 and 5 were sampled 1/18/04 and pools 2, 3, and 4 on 1/22/04. The literature indicates fish abundances vary only slightly between low tides in the same low tide series (Thomson and Lehner 1976; Allen unpublished data), therefore, pools 1 and

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5 were not resampled on the second day. This site was sampled in one day for all other seasons.

The northern most site lies within Leo Carrillo State Park in Malibu, California. The area was protected from collection of intertidal invertebrates by lifeguards and park rangers. Study pools were situated around the perimeter of a south-facing rock outcrop situated 2 m to 5 m above the surrounding sand. Pools were distributed from 0.8 m to 1.9 m above mean lower low water (MLLW). They were the highest with the smallest mean pool surface area of all six sites. Not only were there few alternate pools available that met the criteria for selection, but there were very few other tidepools in general. This site was exposed to high wave energy based on the model and field observations and lacked *Silvetia compressa*.

The Paradise Cove site was located approximately 16 km downcoast of Leo Carrillo. Access to this site was very limited as most adjacent land was privately owned, thus received few visitors. Sand levels fluctuated greatly in the Malibu area. Consequently, it was difficult to find five permanent pools in the 2.4 km expanse of beach downcoast of Point Dume. Observations indicated the study pools were the only permanent pools at this site. They were situated in a row along a narrow, low-lying rock outcrop perpendicular to shore and ranged from -0.3 m to 0.9 m above MLLW. The surrounding area was a series of low-lying rock ridges, boulder fields and sand beaches that extended from the access point at Paradise Cove up coast to Point Dume. The south-facing cove was the most protected from northwesterly wave energy of the six study sites with abundant *Silvetia compressa* and low tidepools.

Resort Point was situated approximately 61 km downcoast of Paradise Cove on the north side of Palos Verdes peninsula. The study site was at the bottom of a very steep cliff and required a walk across a cobble beach to the rocky point, thus it received very few visitors other than local surfers. Intertidal fishes were sampled at this site by Crase (1992) in 1983/84 using the same draining methodology described earlier. The five original study pools were relocated using photographic documentation and re-sampled in the current study. The study pools were on top of and adjacent to a large rocky bench that rose 2 m above the surrounding surge channel and boulder-covered tidal flat in which there were many tidepools. Tidal heights of study pools extended from 0.5 m to 1.8 m above MLLW. Palos Verdes peninsula had very few sandy beaches with the nearest sizable beach approximately 6 km upcoast of the study site. This west-facing site experienced the highest wave energy based on the model and field observations and had the largest pools of the six sites.

White's Point also was located on Palos Verdes peninsula but 10.5 km downcoast of Resort Point. The study site was on the lee side of the point in a southeast-facing cove. This area received little protection from collecting and was very accessible to the public. The site was best characterized as a rocky bench defined by a series of rock ridges. Adjacent to the bench was an expansive boulder field to the southeast. The pools were situated in surge channels formed between rock ridges with the exception of Pool 1 which was located in a small rocky outcrop approximately 60 m downcoast of Pool 2. Study pools were distributed from 0.1 m to 0.9 m above MLLW. Some tidepools occurred lower than the study pools and many were found around the point towards the windward side. White's Point experienced intermediate wave energy.

Little Corona was the next site 50 km downcoast of White's Point just south of Newport Harbor. This marine reserve was protected by the city of Corona del Mar and received many visitors. Study pools were located on a southwest-facing rocky bench that was situated between a small sandy beach up-coast and an expansive boulder field downcoast. This

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bench rose 1 m to 2 m above the surrounding tidal flat and the pools ranged from 0.2 m to 1.0 m above MLLW. Little Corona ranked as the second most hydrodynamically protected site of the six sites sampled.

The most southerly site was Shaw's Cove in Laguna Beach approximately 9.5 km downcoast of Little Corona. The city of Laguna Beach protected the area from collecting. A narrow rocky bench lined the up-coast side of this southwest-facing cove. The bench sat above a sandy beach on the downcoast end by 1 to 2 m. The rocky bench was a relatively flat table of rock that was intermittently scored by surge channels and tidepools. *Silvetia compressa* grew thickly on top of the bench. Pool 0 and 4 were depressions similar to surge channels while the others were situated on top of the bench. Pools extended from 0.03 m to 1.0 m above MLLW. Shaw's Cove received intermediate wave energy.

Species richness and species diversity (Shannon-Wiener Index, H′) were calculated for fish assemblages in each pool for each season, for each site for each season, and overall, for each site:

$$H' = -\sum p_i(\ln p_i) \text{ where } p_i = \text{proportion of species } i.$$

Multiple regression analysis was conducted to assess relationships of species diversity with latitude and wave exposure (mean significant wave height). Multiple regression also was used to evaluate changes in total fish abundance per pool with pool physical characteristics of surface area (SA), volume (Vol), depth, and surface area to volume ratio (SA:Vol). SA alone was significantly correlated with total abundance ($r^2 = 0.34$, $F_{4,23} = 4.012$, $p < 0.05$). Therefore, species abundances were standardized to SA by calculating species densities (individuals/m^2) by averaging the number of fish found in each pool per square meter of pool surface area. One-way Analysis of Variance (ANOVA) was used to test for seasonality of species diversity. We used a two-way ANOVA (STATISTICA 9., StatSoft Inc, Tulsa, OK) to test abundances and densities both for the three most common species (*Clinocottus analis*, *Clinocottus recalvus*, *Girella nigricans*) and for all fishes found by site and season. Abundances and densities were log-transformed to normalize the data. A Tukey post-hoc was then used to assess groupings of the results. Sea urchin and sea star counts were standardized to pool surface area (individuals/m^2) then densities for each were assessed for variation by site using Kruskal-Wallis.

Principal Component Analysis (PCA) was used to identify relationships among 17 environmental variables recorded for each sampling unit. Redundant variables were then removed from the environmental variable matrix used in a later Canonical Correspondence Analysis (CCA) to improve the accuracy of the analysis (STATISTICA 9., StatSoft Inc, Tulsa, OK). Neither PCA nor CCA, which will be discussed later, are significance tests because the ordination scores are not independent of one another and are generally used to describe patterns with no *p*-values generated. Rather than reducing the number of environmental variables to a smaller number of synthetic variables, PCA was used to identify correlations that may exist among environmental variables and eliminate redundancy. The analysis was then grouped by site to suggest how sites corresponded with axes. For this analysis, environmental variable data were log-transformed to improve linearity.

To identify relationships among fish species and environmental variables, a Canonical Correspondence Analysis (CCA) was used. CCA constrains the ordination results of one matrix (in this case species densities) by a second matrix (environmental variables) to identify patterns that may not be observed by simply reviewing the data. This method was chosen over multiple regression because the data are non-parametric (zeroes prevent even transformed data from being normal). Species found once or that represented less than 2%

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of the total catch were eliminated from the analysis (*Artedius lateralis*, *Kyphosus azureus*, and *Apodichthys fucorum*). Environmental variables and species densities were averaged across seasons for each pool. Based on the correlation matrix presented by the PCA, redundant environmental variables were removed from the environmental variable matrix in the CCA. The remaining variables used in the CCA were latitude, pool tidal height, pool temperature, and percent cover of upright macroalgae, surfgrass, boulders, and cobble/shell hash. Surfgrass percent cover was winsorized (Quinn and Keough 2003) for one pool at Paradise Cove (PC01) to reduce impact of the outlier. Environmental variables with r-values greater than 0.350 were plotted.

To identify possible size stratification in pools of *Clinocottus analis*, mean standard length per pool was assessed using two methods. The first regressed mean standard length with tidal height of the pool. Tidal heights were also categorized as either high (0.9–1.9 m), mid (0.5–0.8 m) or low (−0.1–0.4 m). An ANOVA was used to again test mean standard length with tidal category.

Results

Pool surface areas at each site varied greatly; Leo Carrillo, 0.5–1.7 m^2; Paradise Cove, 0.7–3.0 m^2; Resort Point, 4.6–25.3 m^2; White's Point, 0.8–5.9 m^2; Little Corona, 0.7–6.9 m^2; and Shaw's Cove, 1.1–3.1 m^2 (Table 1). Resort Point pools had the highest average surface area of 13.10 m^2 while Leo Carrillo had the lowest at 0.95 m^2. Individual pool surface areas ranged from 0.46 m^2 for Pool 5 at Leo Carrillo to 25.29 m^2 for Pool 2 at Resort Point. Individual pool volumes and average depths also varied considerably from pool to pool (Table 1). Tidal heights of pools (Table 1) ranged from -0.03 m at Paradise Cove to +1.95 m at Leo Carrillo. Fish were found consistently in the highest pool at Leo Carrillo. Due to high wave energy at this site, this pool likely experiences some inundation of water even at high tides below +1.95 m as higher wave energy generally results in higher water levels and wave run-up at the shore (http://cdip.ucsd.edu). The lowest pool (−0.08 m) was only sampled once at Shaw's Cove (January 2004) because it was not isolated long enough to sample regularly.

From January 2004 to February 2005, pool temperatures ranged from a minimum of 13.3 °C at Paradise Cove in January 2004 to a maximum of 20.2 °C at Resort Point in July 2004. Maximum mean pool temperatures occurred during the summer in July 2005 and minimum during the winter in January 2004. No thermal stratification among the sites was evident. Sea surface temperatures for the Southern California Bight during the study period were measured by NOAA Buoy 46025 and monthly means ranged from a low of 14.2 °C in January 2004 to a high of 21.2 °C in July of 2004. Mean pool temperatures for each site typically were lower than the hourly sea surface temperature recorded by the buoy for the hour at which low tide occurred. The exception to this for most sites occurred during winter samplings when pools generally separated from the ocean later in the afternoon and thus had more daylight hours to warm.

Dissolved oxygen (DO) levels (Table 2) varied greatly from site to site and pool to pool with the maximum level of 17.08 mgO_2/L recorded at Resort Point in January 2004 and the minimum of 0.82 mgO_2/L at Leo Carrillo in May 2004. Mean site DO levels were highest in January 2004, lowest in May 2004 and July 2004, then increased December 2004. This trend corresponds with daytime and nighttime low tides; pools become supersaturated during the day and hypoxic at night (Martin and Bridges 1999). Interestingly, fishes occupied pools even with very low DO levels. If conditions become hypoxic, many

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Table 1. Physical characteristics of tide pools: mean surface area, mean depth, volume, surface area to volume ratio, and tidal height for each of the 29 pools sampled.

Site	Pool	Mean SA (m^2)	Mean depth (m)	Volume (m^3)	SA:Vol	Tidal heightand category (m)	Tidal height designation
Leo Carrillo	1	1.003	0.122	0.12	8.19	1.6	high
	2	0.783	0.2	0.16	5.00	0.9	high
	3	0.819	0.174	0.14	5.76	1.9	high
	4	1.683	0.142	0.24	7.05	0.8	mid
	5	0.461	0.148	0.07	6.78	0.8	mid
Paradise Cove	1	3.043	0.194	0.59	5.15	0.0	low
	2	1.882	0.185	0.35	5.41	0.4	low
	3	1.952	0.109	0.21	9.17	0.2	low
	4	1.456	0.16	0.23	6.25	0.9	high
	5	0.664	0.124	0.08	8.06	0.8	mid
Resort Point	1	13.082	0.433	5.67	2.31	1.7	high
	2	25.29	0.378	9.56	2.65	0.9	high
	3	12.397	0.177	2.202	5.65	0.5	mid
	4	10.116	0.185	1.87	5.41	0.6	mid
	5	4.595	0.41041	1.88	2.44	1.8	high
White's Point	1	3.098	0.117	0.36	8.54	0.1	low
	2	0.768	0.091	0.07	11.05	0.5	mid
	3	5.892	0.14	0.83	7.12	0.9	high
	4	1.387	0.103	0.14	9.74	0.4	low
Little Corona	1	6.881	0.154	1.06	6.49	0.5	mid
	2	3.819	0.0985	0.38	10.15	0.7	mid
	3	2.447	0.1255	0.31	7.97	0.2	low
	4	0.729	0.2634	0.19	3.80	1.0	high
Shaw's Cove	0	2.761	0.123	0.34	8.16	0.4	low
	1	1.598	0.221	0.35	4.52	0.3	low
	2	2.808	0.089	0.25	11.28	0.8	mid
	3	2.5	0.33	0.83	3.03	-0.1	low
	4	1.104	0.144	0.16	6.97	0.0	low
	5	3.142	0.121	0.38	8.25	1.0	high

intertidal fishes, including *Clinocottus analis* and *Clinocottus recalvus*, can emerge from the water to breathe air (Martin 1995; Martin and Bridges 1999; Martin 2014). Mean DO levels for each pool ranged from 2.7 to 8.6 mgO_2/L with an overall mean of 6.0 + 1.4 mgO_2/L. No levels were recorded February 2005 because a dissolved oxygen meter was not available.

Monthly mean maximum significant wave heights (m) (MSWH) were generated for each site (Fig. 2) for the period March 1998 to March 2005 using the model created by the Coastal Data Information Program allowing a comparison of wave energy between sites. Resort Point experienced the highest amount of wave energy with an overall mean height of 0.21 m while Paradise Cove was the most sheltered with a mean of 0.13 m. The same model was used to generate MSWH for Piedras Blancas (Blanchette unpublished data) on the central California coast. This site experienced high wave energy with an overall mean

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Table 2. Physical and chemical characteristics of each tide pool: mean temperature (°C), pH, Dissolved Oxygen (mgO_2/L), and salinity (ppt) for each of the 29 pools sampled.

Site	Pool	Temp (°C)	pH	DO (mgO_2/L)	Salinity (ppt)
Leo Carrillo	1	15.6	8.1	7.5	35.2
	2	15.2	7.9	3.3	35.4
	3	15.7	8.0	4.4	35.6
	4	15.7	7.9	2.7	35.2
	5	15.6	8.0	3.0	35.5
Paradise Cove	1	15.8	8.3	6.6	36.2
	2	16.0	8.2	6.8	35.8
	3	16.2	8.2	6.4	35.6
	4	15.3	8.1	6.0	35.4
	5	15.8	7.9	5.0	35.6
Resort Point	1	17.0	8.3	6.8	35.4
	2	17.1	8.3	6.7	35.0
	3	17.0	8.2	5.7	34.8
	4	16.9	8.2	7.4	35.4
	5	17.2	8.4	8.6	35.4
White's Point	1	16.8	8.1	7.0	35.0
	2	16.4	8.1	7.1	35.2
	3	15.9	8.0	6.5	35.4
	4	16.5	7.8	4.5	33.8
Little Corona	1	16.9	8.0	5.2	35.2
	2	17.1	8.0	5.8	35.4
	3	17.0	8.0	5.9	35.0
	4	17.1	8.1	6.7	35.0
Shaw's Cove	0	17.8	8.4	6.7	35.7
	1	17.1	8.4	7.5	35.8
	2	16.7	8.1	4.6	35.4
	3	15.2	8.2	7.1	35.5
	4	16.7	8.3	5.4	36.0
	5	16.8	8.2	6.3	35.2

(1998 to 2002) of approximately 0.59 m. In comparison, the six southern California sites sampled in this study experienced much lower wave energy with the highest monthly mean of all sites being only 0.37 m at Resort Point. The outcome of the model agrees with field observations.

In the five sampling dates from January 2004 to February 2005, 3,043 fishes were captured weighing a total of 19.81 kg and belonging to ten species from six families (Table 3 and 4). *Clinocottus analis* dominated abundance in all seasons at 68.1% of the total catch followed by *Girella nigricans* at 10.5%, *Clinocottus recalvus* at 6.1%, and *Hypsoblennius gilberti* at 5.6% (Table 3). *Clinocottus analis* also dominated in biomass at 68.4% of the total biomass followed by *Clinocottus recalvus* at 12.2%, *Girella nigricans* at 10.9%, and *Hypsoblennius gilberti* at 4.7% (Table 4). These four species accounted for 90.3% of the total number of fishes captured and 96.2% of the total biomass. The overall low species richness

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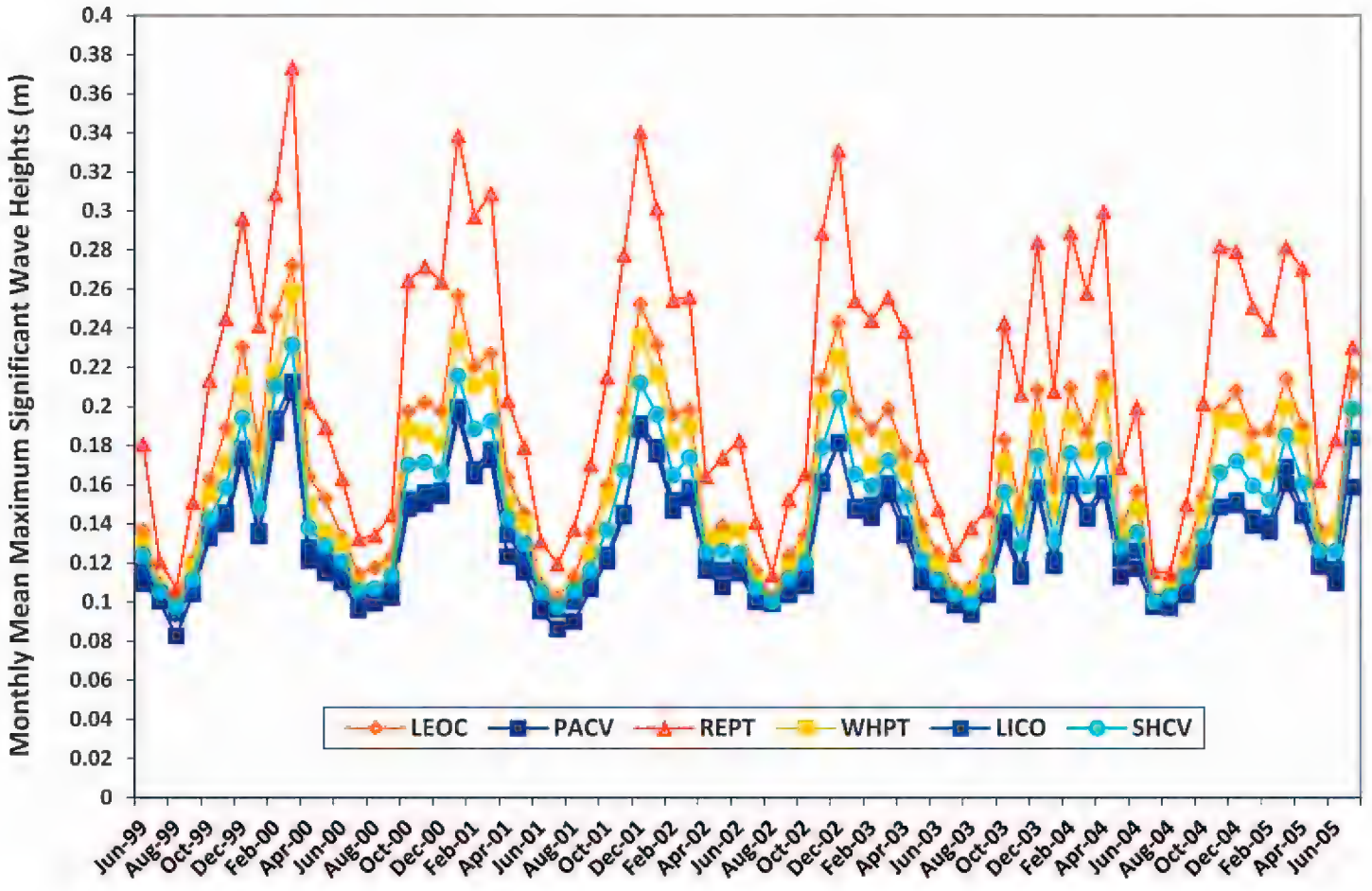

Fig. 2. Monthly mean maximum significant wave heights (m) were generated for each site for the period June 1999 to June 2005. A model developed by the Coastal Data Information Program at Scripps Institution of Oceanography was used to predict site-specific relative exposures. This model used predicted inshore wave heights generated from the southern California swell model.

and diversity values for total abundance (10, 1.16 respectively) (Table 5) reflect this predominance. The lowest species diversity was found at Leo Carrillo (0.56) while the highest was at the next site to the south Paradise Cove (1.30). The greatest number of species was found both overall and in one sampling season at Paradise Cove (8 and 7 species).

The effects of latitude, wave exposure, and date on species diversity (H′) for each site were examined. H′ decreased as wave exposure increased ($r^2 = 0.29$, $F_{3,26} = 3.620$, $p < 0.02$) and increased with each successive date ($r^2 = 0.29$, $F_{3,26} = 3.620$, $p < 0.05$). Latitude was not a significant factor ($r^2 = 0.29$, $F_{3,26} = 3.620$, $p > 0.05$). H′ was also tested with sampling season to identify any seasonal trends, but this relationship was not significant (ANOVA, $F_{4,25} = 1.541$, $p > 0.05$).

Overall mean densities (individuals/m^2) for each site were highest for all sites January 2004 and lowest for most sites in May 2004 and July 2004. High densities did not persist for the second winter season sampled in February 2005 although some sites did experience a second peak in density in December 2004. Interestingly, fish abundance and density were not redundant metrics. Of the six sites sampled, abundance was highest at Resort Point where density was lowest (Fig. 3), and while abundance was the third lowest at Leo Carrillo, density was highest. Densities did vary by site (ANOVA, $F_{5,107} = 5.857$, $p < 0.001$), but not by season (ANOVA, $F_{4,107} = 1.609$, $p > 0.05$) or by season and site (ANOVA, $F_{20,107} = 0.472$, $p > 0.05$). Densities were significantly higher at Leo Carrillo and White's Point (Tukey post hoc; $p < 0.05$). Overall mean density for each species at each site where they were found again indicates dominance by *Clinocottus analis* at 5.48/m^2 followed by *Clinocottus recalvus* at 4.52/m^2. Because overall densities were calculated for species only

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Table 3. Total abundance of fishes captured by site from January 2004 through February 2005. Sites are listed north to south. LEOC – Leo Carrillo, PACV – Paradise Cove, REPT – Resort Point, WHPT – White's Point, LICO – Little Corona, SHCV – Shaw's Cove.

	Sites							
Species	LEOC	PACV	REPT	WHPT	LICO	SHCV	Total	%
Clinocottus analis	298	178	871	330	213	183	2,073	68.1
Girella nigricans	1	2	98	35	112	70	318	10.5
Clinocottus recalvus	78	1	108				187	6.1
Hypsoblennius gilberti	1	46	1	1	111	10	170	5.6
Gobiesox rhessodon			3	136	14	5	158	5.2
Gibbonsia elegans		59		2	3	4	68	2.2
Oligocottus snyderi	1	63					64	2.1
Kyphosus azureus			3				3	0.1
Artedius lateralis		1					1	0.0
Apodichthys fucorum		1					1	0.0
TOTAL	379	351	1084	504	453	272	3,043	

Table 4. Total biomass (g) of fishes captured by site from January 2004 through February 2005. Sites are listed north to south. LEOC – Leo Carrillo, PACV – Paradise Cove, REPT – Resort Point, WHPT – White's Point, LICO – Little Corona, SHCV – Shaw's Cove.

	Sites							
Species	LEOC	PACV	REPT	WHPT	LICO	SHCV	Total	%
Clinocottus analis	3,428.3	985.2	5,393.8	1,544.6	1,211.8	984.5	13,548.3	68.4
Clinocottus recalvus	1,306.9	15.0	1,104.2				2,426.1	12.2
Girella nigricans	14.0	2.5	980.4	417.1	507.9	229.2	2,151.1	10.9
Hypsoblennius gilberti	10.0	230.0	4.0	4.0	641.7	34.7	924.4	4.7
Gibbonsia elegans		266.1		6.5	25.0	40.3	337.9	1.7
Gobiesox rhessodon			8.0	193.5	20.3	6.3	228.2	1.2
Oligocottus snyderi	5.0	161.3					166.3	0.8
Kyphosus azureus			18.5				18.5	0.1
Artedius lateralis		6.0					6.0	0.0
Apodichthys fucorum		2.0					2.0	0.0
TOTAL	4,764.2	1,668.1	7,508.9	2,165.8	2,406.8	1,295.0	19,808.7	

at the sites where they were captured, *Girella nigricans* and *Hypsoblennius gilberti* were replaced by *Gobiesox rhessodon* at 2.89/m^2 and *Oligocottus snyderi* at 2.04/m^2 in the top four most dense species.

No seasonal pattern was detected in either densities or abundances for the three most abundant species or total fishes found at each site (Abundances: *Clinocottus analis*, $F_{4,128} = 1.418$, $p > 0.05$; *Girella nigricans*, $F_{4,79} = 1.710$, $p > 0.05$; *Clinocottus recalvus*, $F_{4,44} = 0.967$, $p > 0.05$; all fishes, $F_{4,64} = 0.793$, $p > 0.05$. Densities: *Clinocottus analis*, $F_{4,128} = 1.670$, $p > 0.05$; *Girella nigricans*, $F_{4,79} = 2.154$, $p > 0.05$; *Clinocottus recalvus*, $F_{4,44} = 0.228$, $p > 0.05$; all fishes, $F_{4,64} = 1.043$, $p > 0.05$). A general seasonal trend of greater

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Table 5. Seasonal and overall species diversity (H′) and richness (#) at each site. Sites are listed north to south. LEOC – Leo Carrillo, PACV – Paradise Cove, REPT – Resort Point, WHPT – White's Point, LICO – Little Corona, SHCV – Shaw's Cove.

	Sites											
	LEOC		PACV		REPT		WHPT		LICO		SHCV	
	H′	#	H′	#	H′	#	H′	#	H′	#	H′	#
Jan-04	0.55	2	1.12	7	0.52	3	0.56	3	0.97	4	0.49	4
May-04	0.66	2	0.86	4	0.52	3	0.56	3	0.92	4	0.09	2
Jul-04	0.63	2	1.14	5	0.61	4	0.81	4	1.10	3	0.97	4
Dec-04	0.49	3	1.36	4	0.85	5	0.96	4	1.32	5	0.98	5
Feb-04	0.28	4	1.29	4	0.60	3	0.80	3	1.30	5	1.10	5
Overall	0.56	5	1.30	8	0.79	6	0.85	5	1.19	5	0.87	5

overall densities in the fall and winter was apparent (Fig. 3), but not significant (ANOVA, $F_{4,64} = 1.0$, $p > 0.05$).

In five sampling dates, 379 fish were captured at Leo Carrillo weighing 4764.2 g and belonging to five species (Tables 3 and 4). *Clinocottus analis* dominated the assemblage at 78.6% of the total catch and 72.0% of the total biomass followed by *Clinocottus recalvus* at 20.6% and 27.4% respectively (Table 3 and 4). These two cottid species accounted for 99.2% of the total catch and 97.4% of the total biomass captured at this site. These percentages are reflected in low seasonal species diversity (H′) values ranging from 0.28 in February 2004 to 0.66 in May 2004 (Table 5). Leo Carrillo was the only site to experience higher seasonal

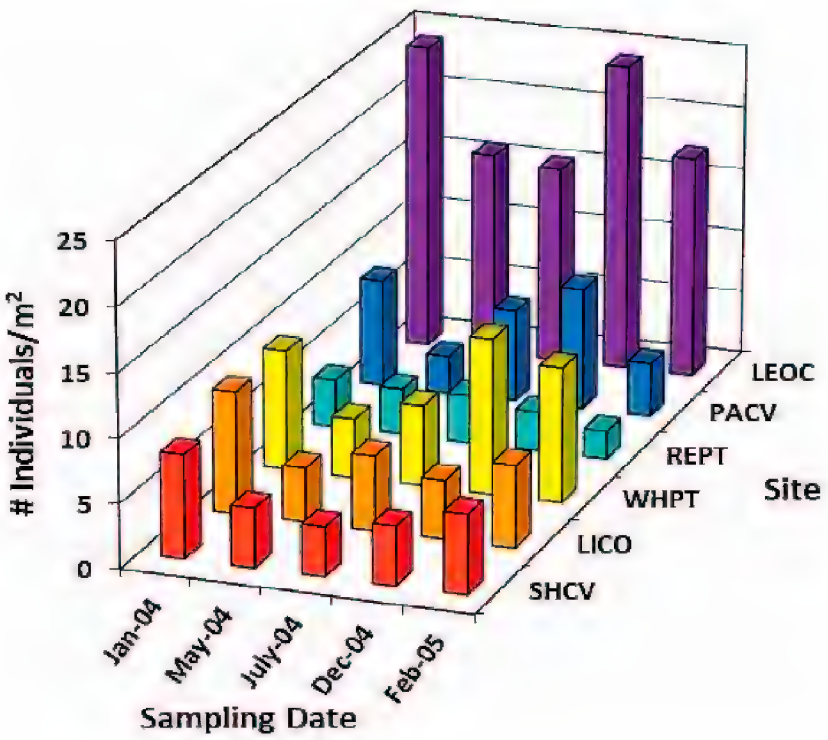

Fig. 3. Mean densities at each site for each season. Densities did vary by site (ANOVA, $F_{5,107} = 5.857$, $p < 0.001$), but not by season (ANOVA, $F_{4,107} = 1.609$, $p > 0.05$) or by season and site (ANOVA, $F_{20,107} = 0.472$, $p > 0.05$). Densities were significantly higher at Leo Carrillo and White's Point (Tukey post hoc; $p < 0.05$). LEOC – Leo Carrillo, PACV – Paradise Cove, REPT – Resort Point, WHPT – White's Point, LICO – Little Corona, SHCV – Shaw's Cove.

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H′ in spring and summer than in fall and winter and had the lowest overall species diversity of 0.56.

A total of 351 individuals were captured at Paradise Cove in five sampling periods weighing 1668.1 g and belonging to eight species. *Clinocottus analis* dominated in both abundance and biomass at 50.7% and 59.0% respectively. *Clinocottus analis* was followed in abundance by *Oligocottus snyderi* at 17.1%, *Gibbonsia elegans* at 16.8% and *Hypsoblennius gilberti* at 13.1%. In biomass, *Clinocottus analis* was followed by *Gibbonsia elegans* at 16.0%, *Hypsoblennius gilberti* at 13.8%, and *O. snyderi* at 9.7%. Greater species evenness is reflected in higher seasonal species diversity (H′) values ranging from 0.86 in May 2004 to 1.36 in December 2004. Paradise Cove had the highest overall H′ of the six sites (1.30).

The greatest number of individuals was captured at Resort Point probably due to the large size of the pools sampled. In the five sampling dates for this study, 1,084 fishes were captured weighing 7,508.9 g and belonging to six species. *Clinocottus analis* comprised 80.3% of the total catch and 71.8% of the total biomass followed by *Clinocottus recalvus* at 10.0% and 14.7%, *Girella nigricans* at 9.0% and 13.0%. These three species together comprised 99.3% of the total catch and 99.5% of the total biomass captured. The overall species diversity (H′) at Resort Point was 0.79 with the highest seasonal H′ in December 2004 at 0.96.

A total of 504 fishes were captured at White's Point weighing 2165.8 g and belonging to five species. *Clinocottus analis* dominated in both abundance and biomass at 65.5% and 71.3% respectively. *Clincottus analis* was followed in abundance by *Gobiesox rhessodon* at 27.0%, and *Girella nigricans* at 7.0%, and was followed in biomass by *Girella nigricans* at 19.3%, and *Gobiesox rhessodon* at 8.9%. These three species made up 99.5% of the total abundance and 99.5% of the biomass. Seasonal species diversity (H′) was greatest in December 2004 and the overall H′ was 0.85.

At Little Corona, 453 individuals were captured weighing 2406.8 g and belonging to five species. Again, *Clinocottus analis* dominated in both abundance (47%) and biomass (50.3%) followed by *Hypsoblennius gilberti* at 24.5% and 26.7%, and *Girella nigricans* at 24.7% and 21.1% respectively for both species. These three species comprised 96.2% of the total catch and 98.2% of the total biomass. Seasonal species diversity (H′) at Little Corona ranged from a low of 0.92 in May 2004 to a high of 1.32 in December 2004. Overall H′ was the second highest at 1.19.

The least number of fishes was captured at Shaw's Cove, 272 individuals weighing 1295.0 g and belonging to five species. Not surprisingly, *Clinocottus analis* again dominated this assemblage in abundance and biomass as well at 67.2% and 67.3% respectively. *Girella nigricans* followed at 25.7% and 17.7% respectively. These two species accounted for 92.9% of the total abundance and 85.0% of the total biomass. Seasonal species diversity (H′) plummeted to a low of 0.09 in May 2004 but recovered for a high of 1.10 in February 2005. Overall H′ was 0.87.

Principal Component Analysis determined Factor 1 (Axis 1) represented pool surface area ($r = 0.77$) and depth ($r = 0.75$) while Factor 2 (Axis 2) represented latitude ($r = -0.80$), pool temperature ($r = 0.53$) and associated biotic and abiotic factors (Fig. 4). These two factors accounted for 43% of the variation. Sea star density ($r = -0.45$) and surfgrass percent cover ($r = -0.39$) were positively correlated with latitude (notice r value of latitude) while pool temperature and cobble/shell hash percent cover ($r = 0.47$) were negatively correlated meaning northern sites tended to have more sea stars and surfgrass with cooler pool temperatures while southern sites tended to have pools characterized by cobble/shell hash bottoms and warmer pool temperatures.

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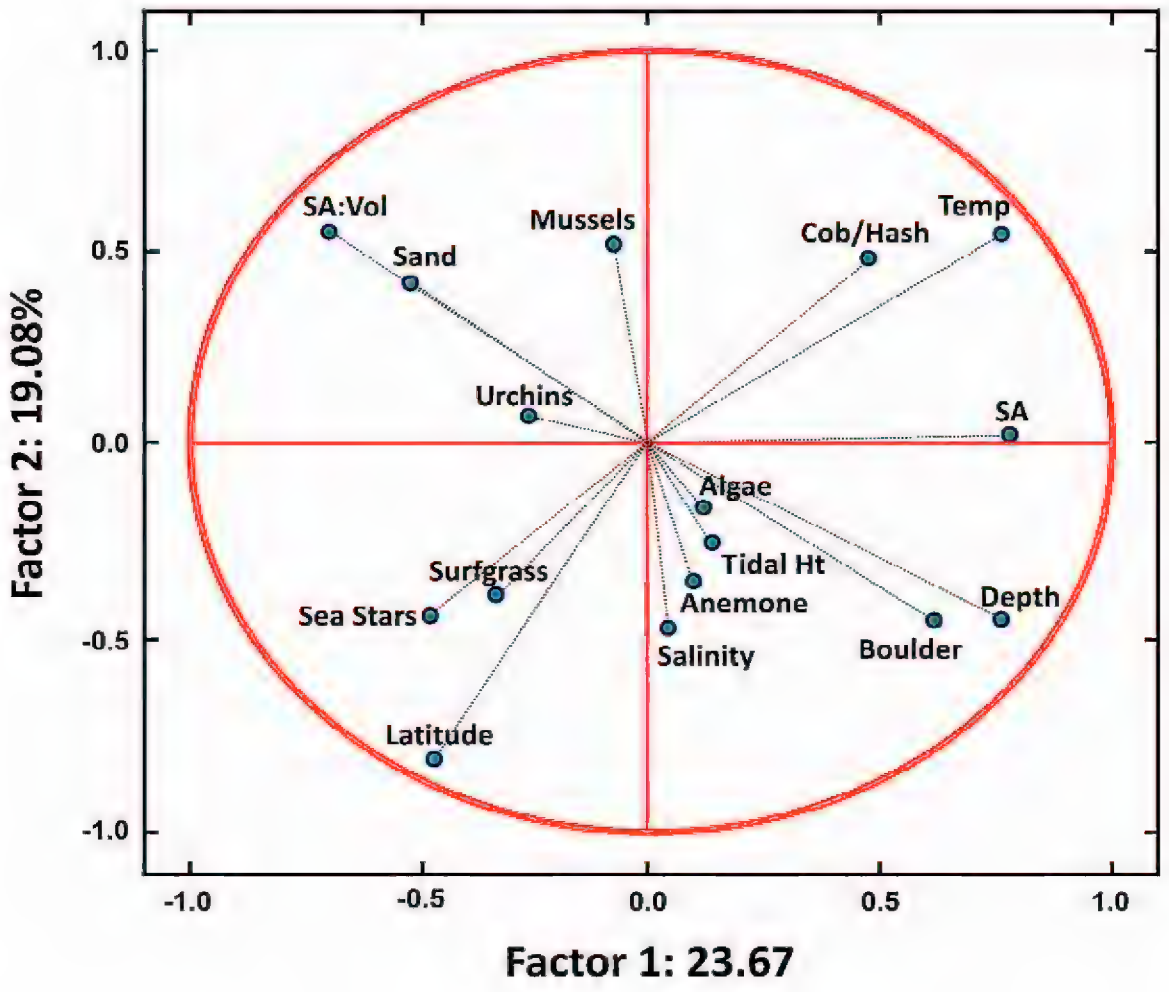

Fig. 4. Projection of the variables on the factor plane using Principal Component Analysis (PCA) to represent correlations among environmental variables. For each pool, 17 environmental variables were measured during each sampling. Data were averaged across seasons for each pool. PCA was used to assess relationships between environmental variables to eliminate redundant variables from the environmental variable matrix used later in a Canonical Correspondence Analysis (CCA). Temperature and cobble shell hash percent cover correlated positively with each other but negatively with latitude.

Sampling units also were grouped by site and evaluated for environmental variable associations (Fig. 5). Resort Point (RP) had the largest, deepest pools of all six sites. White's Point (WP) and Leo Carrillo (LC) grouped about the same in regard to pool size and depth but, WP was characterized by cobble/shell hash substrate and warmer pool temperatures while LC had a greater density of sea stars. Paradise Cove (PC) also was characterized with sea stars and surfgrass. PC and Shaw's Cove (SC) were similar in regard to size and depth of pools, but SC was better described as greater cobble/shell hash percent cover and warmer pool temperatures.

Canonical Correspondence Analysis (CCA) yielded two significant axes in assessing relationships between fish species and environmental variables. Axis 1 was correlated positively with tidal height and negatively with surfgrass percent cover (Fig. 6). *Gibbonsia elegans* and *Oligocottus snyderi* were placed to the far left, reflecting their association with surfgrass and low pools. Axis 2 was correlated positively with latitude and negatively with temperature and percent cover of cobble/shell hash. *Clinocottus recalvus* and *O. snyderi* were associated with northern sites and cooler pool temperatures. *Girella nigricans* and *Gobiesox rhessodon* were associated with southern sites, warmer pool temperatures and cobble/shell hash bottoms. *Clinocottus analis* occurred in the center of both axes indicating it is found in all sampled pool types, temperatures and latitudes. All of these results follow associations observed in the field. These two axes explain 48.1% of the variance (26.7% and 21.4% respectively).

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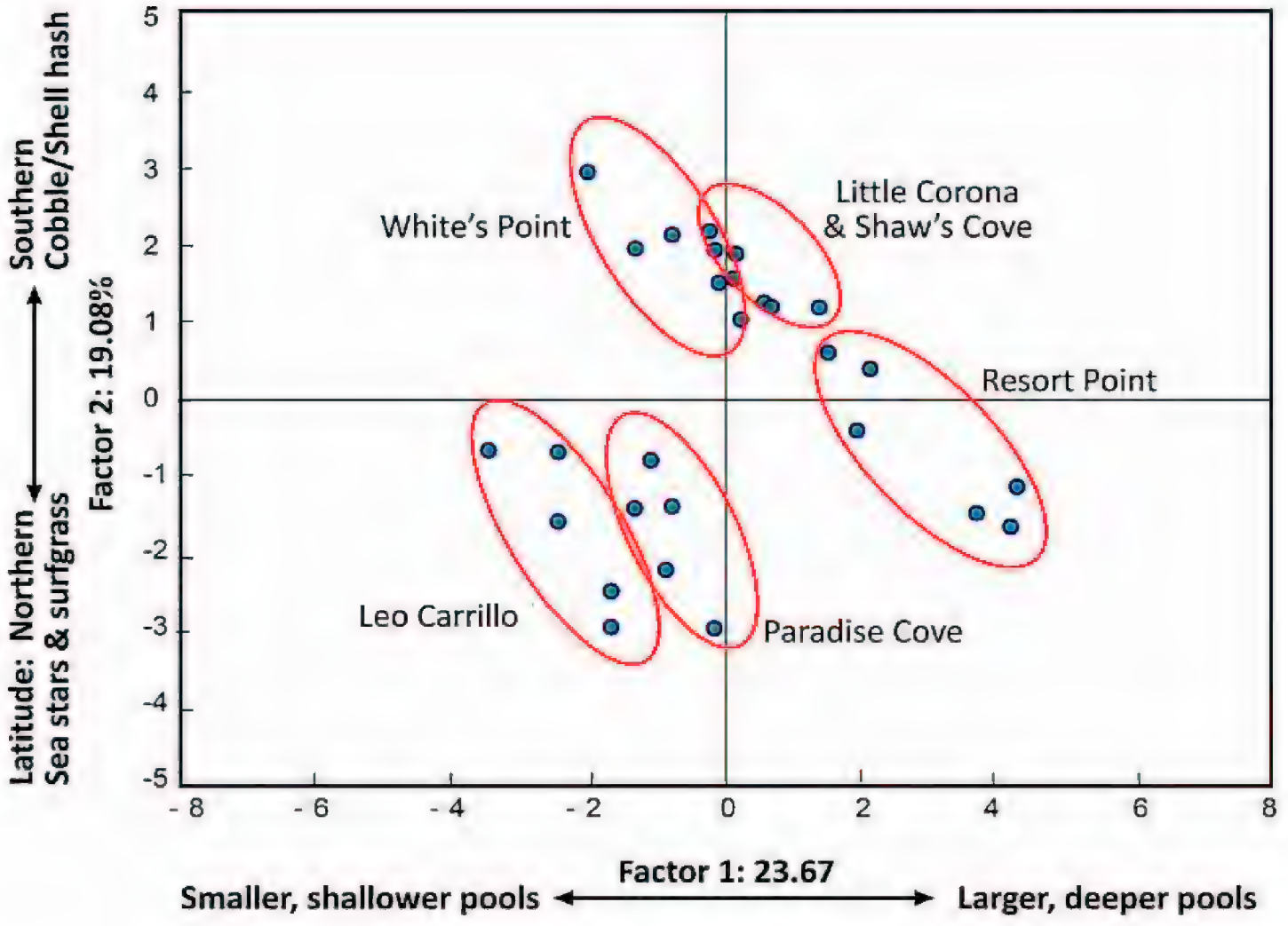

Fig. 5. PCA results of projection of the sampling units (cases) on the environmental variable-plane (factor-plane). Axis 1 represented pool surface area and depth while Axis 2 represented latitude, temperature and associated biotic factors. Sea star density and surfgrass percent cover were positively associated with latitude while temperature and cobble/shell hash percent cover were negatively associated. Pools of sites that associated with the environmental extremes are circles in red. Resort Point (RP) had the largest, deepest pools of all six sites. White's Point (WP) and Leo Carrillo (LC) grouped about the same in regard to Axis 1; however, WP was characterized by warm temperatures and cobble/shell hash pool bottoms while LC had a greater density of sea stars. Paradise Cove (PC) also tended to associate with more sea stars and surfgrass. PC and Shaw's Cove (SC) tended to be similar in regard to size and depth of pool, but SC could be better described as greater cobble/shell hash percent cover with warmer pool temperatures.

Size frequencies were assessed for the five most abundant species (*Clinocottus analis*, *Girella nigricans*, *Clinocottus recalvus*, *Hypsoblennius gilberti*, and *Gobiesox rhessodon*) to identify seasonal recruitment patterns. All individuals captured in one season for each species were grouped into 10 mm size classes (5 mm for *Gobiesox rhessodon*) (Fig. 7 and 8). Abundance of *Clinocottus analis* was highest in Jan 2004, but the greatest proportion of individuals less than 25 mm occurred in Dec 2004 and Feb 2005 (Fig. 7). All *Girella nigricans* captured were juveniles. The highest number of *Girella nigricans* and the largest proportion of individuals less than 35 mm were found in Dec 2004 (Fig. 7). Individual *Clinocottus recalvus* were rarely found smaller than 45 mm thus only one recruitment pulse was detected in Jan 2004 (Fig. 7). Abundance of *Hypsoblennius gilberti* was highest in July 2004. The greatest proportion of individuals less than 25 mm occurred in Jan 2004 (Fig. 8). Both abundance of *Gobiesox rhessodon* and proportion of individuals smaller than 22 mm peaked in Dec 2004 (Fig. 8).

Clinocottus analis was the only species found in great enough abundance to assess size frequencies for recruitment pulses at each site (Fig. 9). Interestingly, in January 2004, only the three southern sites experienced greater proportions of individuals smaller than 27 mm

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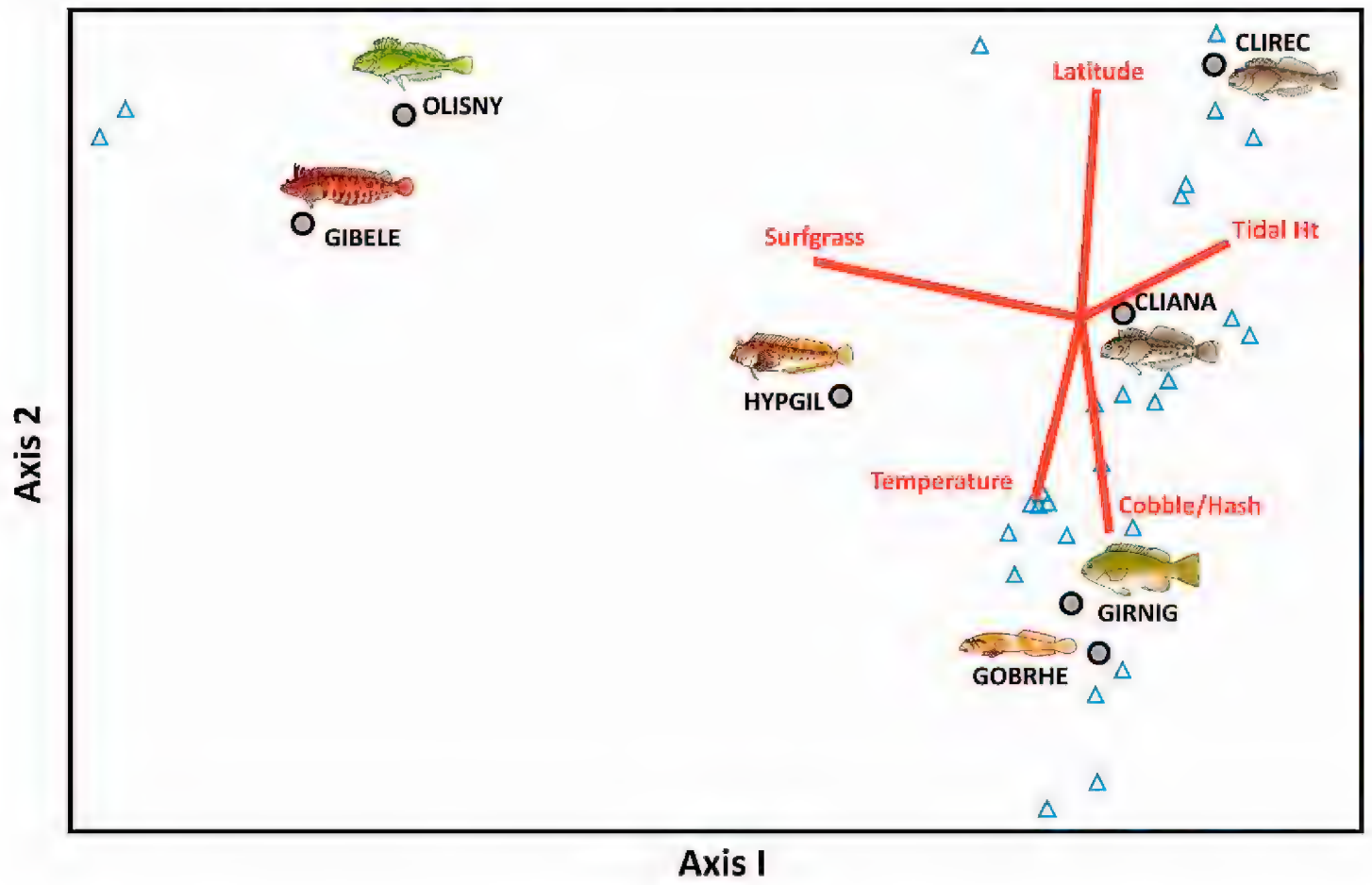

Fig. 6. Canonical Correspondence Analysis (CCA) of species densities and environmental variables (Δ = sampling units, + = species). Axis 1 in the negative direction represents *Gibbonsia elegans* (GIBELE), and *Oligocottus snyderi* (OLISNY) which correlate positively with surfgrass and negatively with tidal height. Axis 2 positively represents *Clinocottus recalvus* (CLIREC) and *O. snyderi*, and negatively *Girella nigricans* (GIRNIG) and *Gobiesox rhessodon* (GOBRHE). The cottid species positively correlate with northern sites while GIRNIG correlates with southern sites and cobble/shell hash percent cover.

(SL). Recruitment occurred at only Shaw's Cove in July 2005 and only White's Point in December 2004. Individuals less than 27 mm were found at all sites during the February 2005 sampling period except Leo Carrillo. Mean standard length of *Clinocottus analis* was not correlated with pool tidal height ($r^2 = 0.008$, $F_{1,128} = 1.113$, $p > 0.2$) nor was there a significant difference in standard length between tidal height categories (ANOVA, $F_{2,127} = 1.222$, $p > 0.2$).

Discussion

In the present study, ten species of fishes were captured in five samples at six sites in the central portion of the Southern California Bight. This is fewer than other rocky intertidal fish surveys done at the southern end of the bight and far fewer than surveys of central and northern California. A study conducted at False Point and Ocean Beach, San Diego (Davis 2000) collected 15 species in 18 samples, but only six were considered common while a second study at Cabrillo National Monument, San Diego (Craig and Pondella 2006) collected 12 species in four samples. These surveys reflect overall low species richness at southern California sites as opposed to species rich central and northern California rocky intertidal benches. Four sites surveyed in the Half Moon Bay area of northern California (Yoshiyama 1981) yielded 24 species representing nine families, and 29 species were collected in 15 samples at Dillon Beach north of the San Francisco Bay area (Grossman 1982). Repeated sampling at San Simeon from 1978 to 1983 yielded 28 species from ten families (L.G. Allen and M.H. Horn unpublished). Differences in species richness be-

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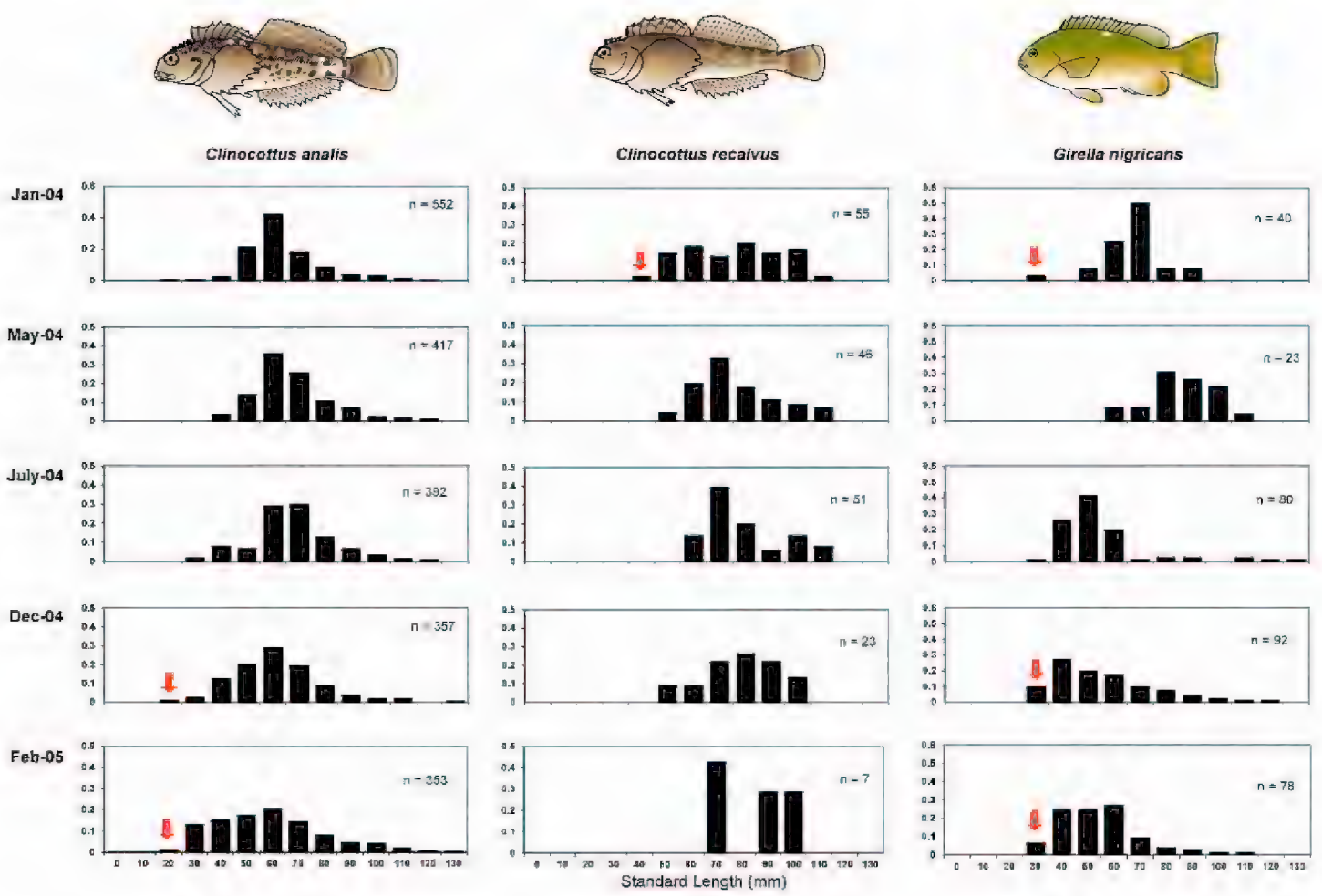

Fig. 7. Size frequency charts of the three most abundant species, *Clinocottus analis*, *Clinocottus recalvus,* and *Girella nigricans*. Abundance of *Clinocottus analis* was highest in Jan 2004, but the highest proportion of individuals under 25 mm occurred in Dec 2004 and Feb 2005. Abundance and proportion of small juveniles of *Girella nigricans* peaked in Dec 2004. Individual *Clinocottus recalvus* were rarely found smaller than 50 mm. Arrows indicate newly recruited size classes.

tween this and other studies of southern California tidepools may be attributable to fewer samples of higher tidepools during this study, perhaps reduced availability of quality habitat at the sites selected or differences in collection methods. The more likely explanation may be that the two San Diego studies were conducted in an area now recognized as the warmer Californian province while our sites lie within the California Transition Zone (CTZ) of the Oregon Province (Briggs and Bowen 2012).

All studies conducted in California rocky intertidal pool habitats (Yoshiyama et al. 1986; Yoshiyama et al. 1987; Crase 1992; Davis 2000) using comparable methods find fish assemblages dominated by cottid species. This study is no exception. Cottidae comprised 74.2% of all fishes found and 80.6% of fish biomass. In fact, Cottidae dominated so strongly that species diversity was consistently low at all sites for all sampling dates.

Motivated by extreme El Niño Southern Oscillation (ENSO) effects, specifically elevated sea surface temperatures and sea levels, Davis (2000) compared two tidepool assemblages in San Diego over time. She concluded that temperature changes caused variations in abundances of particular species but showed little long-term effects. A reduction in the recruitment of *Clinocottus analis*, the dominant species in non-El Niño years, and an increase in abundance of warm-temperate species, such as *Paraclinus integripinnis*, produced greater species evenness during the ENSO event. In total abundance, *Clinocottus analis* was followed by *Girella nigricans* and *Gobiesox rhessodon*, both warm-temperate species. Craig and Pondella (2006) studied intertidal fishes at Cabrillo National Monument, San Diego in three "use zones" that varied in visitor access and thus human-induced disturbance.

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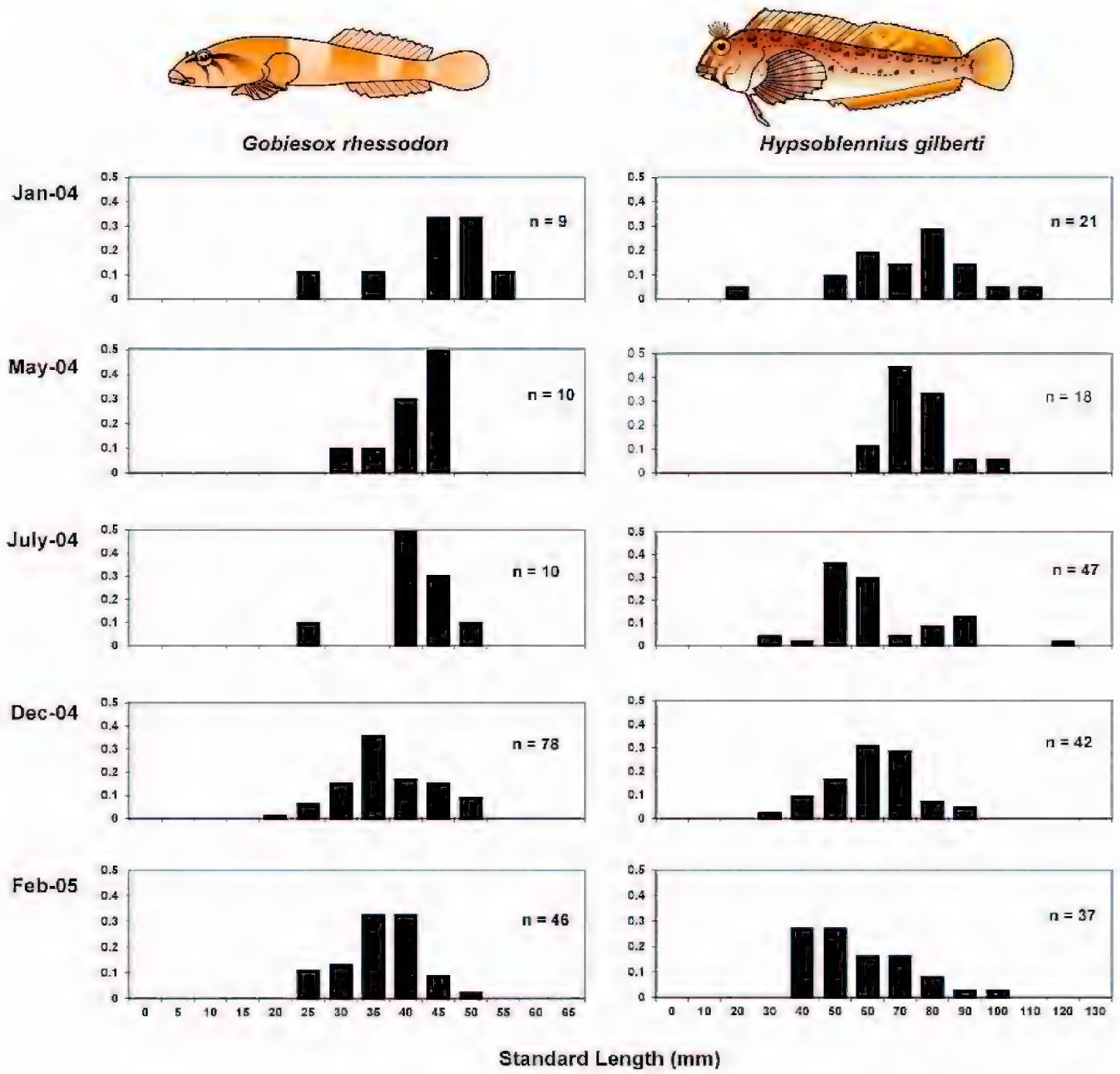

Fig. 8. Size frequency charts of the fourth and fifth most abundant species, *Hypsoblennius gilberti* and *Gobiesox rhessodon*. Abundance of *Hypsoblennius gilberti* was highest in July 2004. The greatest proportion of individuals less than 25 mm occurred in Jan 2004, but not again in the second winter sampling February 2005. Both abundance of *Gobiesox rhessodon* and proportion of individuals smaller than 25 mm peaked in Dec 2004.

They found no significant difference among assemblages of the different zones. These sites were also dominated by *Clinocottus analis* as in Davis' (2000) study, however *Gibbonsia elegans* and the warm-temperate species *Girella nigricans* ranked second and third in abundance. Both studies described sites in San Diego, an area that receives influence from both the southern warm-temperate Californian biogeographic province and the northern cold-temperate Oregonian province (Stepien et. al. 1991). Intertidal fish species found in this area reflect an overlap of these two provinces thus species richness would be greater than sites located outside of this overlap along the central coast of the Southern California Bight.

Certain species were found in varying abundance in different areas of the study region. *Girella nigricans* was quite common at the four most southern sites, but only three individuals were found throughout the study at the two northern sites (Leo Carrillo and Paradise

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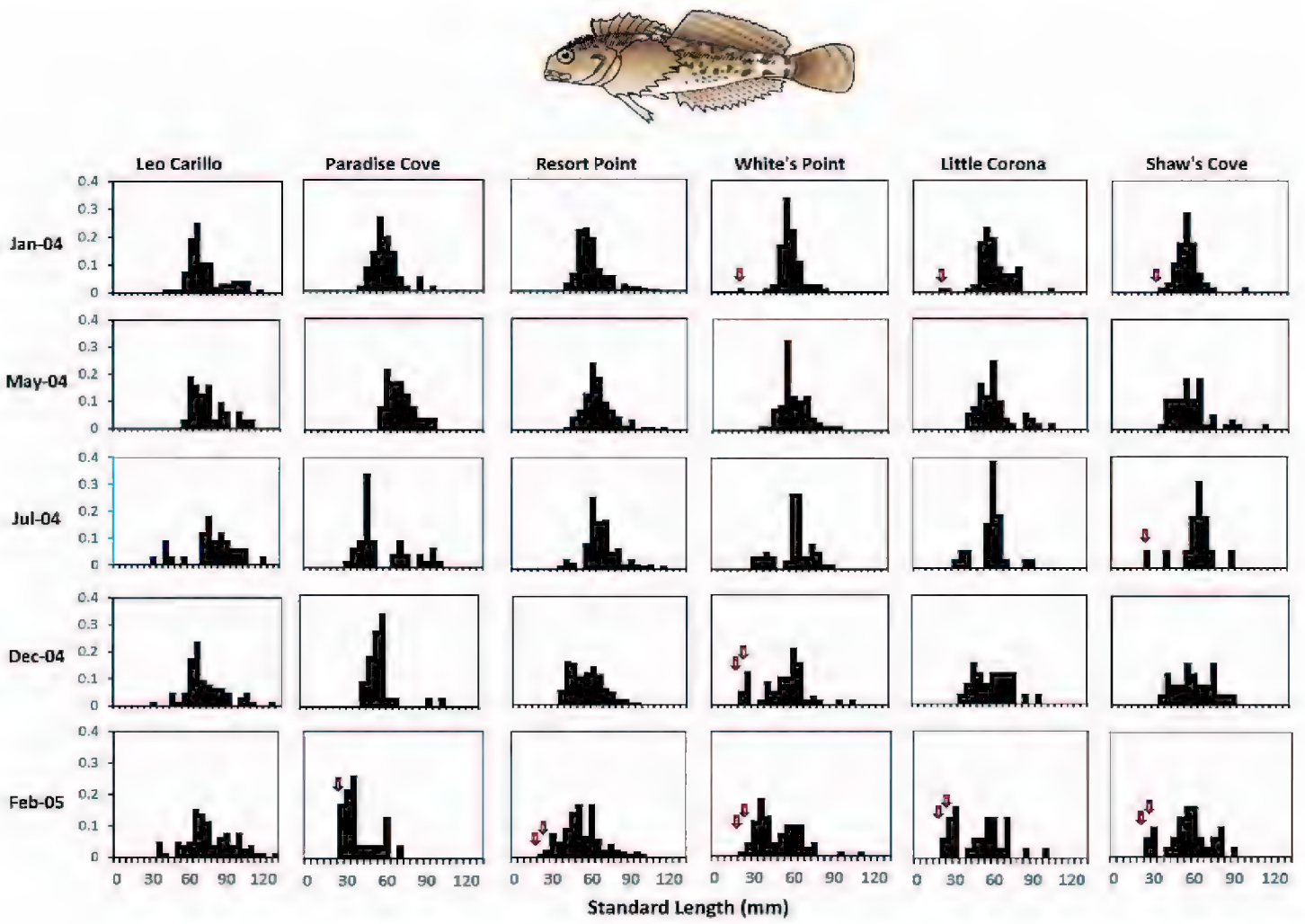

Fig. 9. Size frequency charts of *Clinocottus analis* at the six study sites over five sampling dates. Recruitment (individuals less than 27 mm indicated by red arrows) occurred primarily in early winter at most sites with some regional variation as new recruits were only found at the three southern sites in January 2004. Some recruitment did occur in July 2004 at Shaw's Cove and in December 2004 at White's Point.

Cove). During site reconnaissance three *Girella nigricans* were observed in Pool 4 at Leo Carrillo, but none were found in that pool during sampling. Temperature likely influences this trend as the habitat sampled at the two northern sites is comparable to the southern sites. A large expanse of sandy beach extends along Santa Monica Bay separating the Malibu sites from the Palos Verdes peninsula. However, this is not likely a factor in larval dispersal as adults are not limited strictly to the intertidal. Another explanation might be that greater niche segregation occurred at the two northern sites which limited *Girella nigricans* to shallow ephemeral pools in a boulder/cobble area not sampled.

Clinocottus recalvus was found in abundance at two of the six sites, Resort Point and Leo Carrillo, and once at only one other site, Paradise Cove. The occurrence of *Clinocottus recalvus* at only northern sites may reflect its cool water affinity. However, Resort Point and Leo Carrillo are also the two most wave exposed sites which may indicate *Clinocottus recalvus* associates with high wave energy. Collections from two tidepools in Lunada Bay, the protected cove adjacent to Resort Point, during November 2003 (D. Pondella unpublished) found no *Clinocottus recalvus*. Obviously more collections are needed to test this hypothesis. *Oligocottus snyderi* was captured in abundance only at Paradise Cove, and one individual was captured at Leo Carrillo. This species is known to associate with surfgrass (Nakamura 1976) and cool water. While Leo Carrillo experiences cool water temperatures and has surfgrass as does Paradise Cove, none of the pools sampled actually contained surfgrass. Thus, this species may occur at Leo Carrillo, but only in surfgrass beds.

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Rare and unusual species collected during this study included *Apodichthys fucorum*, *Artedius lateralis*, and *Kyphosus azureus*. According to Horn and Martin (2006), *Apodichthys fucorum* has never been recorded in tidepools in southern California. Only one individual was found throughout the study at Paradise Cove in a pool with surfgrass coverage. *Artedius lateralis* was also only captured once during this study at Paradise Cove. Cryptic fish studies indicate this species is common in the subtidal (coralline sculpin, Froeschke et al. 2005) which may indicate a preference for either the very low intertidal or subtidal environment. *Kyphosus azureus* was found in December 2004 during this study and in 1984 (Crase 1992). This warm-temperate species was also observed in low pools not sampled at Shaw's Cove.

Wave exposure of a site appears to exhibit the greatest influence on species diversity (H′) with diversity increasing at sites with lower wave energy. The three sites that experienced the lowest mean significant wave heights (Paradise Cove, Little Corona, and Shaw's Cove) also had the highest H′. These findings are contrary to Gibson (1972) whose exposed site had an H′ of 2.05 and a sheltered site of 1.52. Whether species diversity of fishes is affected directly by wave energy or indirectly by presence/absence of other organisms requires further investigation. Higher H′ did occur at Leo Carrillo during the summer sampling than other months. Because tidepools at this site are located on a bedrock outcrop that juts into the surf zone, they typically experience high wave action which drops off in July and August. Also, during the summer, tides are the highest of the year. This decrease in wave energy and/or increase in sea level might allow other species to make use of these pools.

Different results were obtained when assessing densities of fishes rather than abundances. This is likely more than an effect of standardizing for pool size. Resort Point is characterized by very large pools, of which there are many. Alternately, Leo Carrillo has very few small pools. Abundances standardized to pool size may be reflecting quality and availability of pool habitat found on the rocky bench at high tide rather than that found in pools during low tide. This raises the question, if a funneling effect does impact abundances of intertidal fishes found in tidepools, are assemblages better described by abundance or density. For example, between sites, if the quality and availability of habitat surrounding pools on the rocky bench is similar, i.e. habitat available at high tide, a given area can support a certain number of fish. If only a few pools are available at low tide, fishes must occupy pools in greater density than if many pools are available. Thus, rocky intertidal areas with many large pools registered high abundances due to the size of the pool, but low densities due to the availability of pools.

Gibbonsia elegans and *Oligocottus snyderi* exhibited a strong association with surfgrass and low pools. The three cottid species encountered (*Clinocottus analis*, *Clinocottus recalvus*, and *Oligocottus snyderi*) grouped together and were associated with northern sites as well as cooler pool temperatures. *Girella nigricans* and *Gobiesox rhessodon* related to southern sites, warmer pool temperatures and pools with cobble/shell hash bottoms. These associations reflect the general temperature preferences and distribution for these fish families. Cottidae is a cool-temperate family found in greatest richness in northern California while kyphosids (sea chubs) and gobiesocids (clingfishes) are characterized as warm-temperate families with their northern limits in southern to central California (Horn and Martin 2006).

Other species of the Cottidae are known to spend approximately 2 months in the plankton as larvae then recruit to the intertidal between 10 and 20 mm from spring to late summer (Pfister 1999). Davis and Levin (2002) detected recruitment pulses of *Clinocottus analis* in all of their quarterly samples, indicating this species recruited year-round during their

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study at two San Diego sites. However, the authors categorized all individuals under 35 mm as recruits. Size frequencies for *Clinocottus analis* at each site during the present study indicated recruitment (individuals less than 25 mm) occurred once a year in the early winter, although, recruitment occurred at only the three southern sites in January 2004 indicating regional variation. When all individuals captured for each season were combined, the greatest proportion of small individuals were found during the late fall and early winter sampling dates.

Small individuals of *Girella nigricans* and *Gobiesox rhessodon* were found during the December 2004 sampling date which also indicated peak recruitment in late fall or early winter. *Hypsoblennius gilberti* recruited most during the July 2004 sampling date. Patterns were less clear for *Clinocottus recalvus*. Too few small individuals were collected to indicate any possible recruitment seasonality. Because dynamic environmental conditions have been shown to impact recruitment success for intertidal fish species, greater replication of sampling seasons over several years is necessary to determine definitive patterns. Vertical size stratification of *Clinocottus analis* was not found during this study. This is likely due to the limited number of pools sampled at each site in a relatively narrow tidal height range rather than an actual reflection of size disbursement of individuals.

Given the highly variable environment that characterizes the rocky intertidal, it is interesting that patterns were detected at all. Results of this study demonstrate that assemblages of intertidal fishes are somewhat predictable. First, some species' northern and southern range limits are located in the Southern California Bight. Three species of cool-temperate cottids were found at the three northern sites while only *Clinocottus analis* was found at southern sites. The warm-temperate kyphosid, *Girella nigricans*, was found in very low abundance at the two northern-most sites but was quite common at sites to the south. Second, more species are found in greater evenness at sites with less wave energy. The three sites that experienced the lowest mean significant wave height also had the highest species diversities. Third, some species associate with particular environmental factors within a pool such as *Gibbonsia elegans* and *Oligocottus snyderi* with surfgrass. Fourth, the size and availability of pools at a given area will likely impact the number and density of a species differently. Lastly, rocky intertidal assemblages within the Southern California Bight will surely be dominated by *Clinocottus analis*. The central portion of the bight is less species-rich than either the northern end, which receives influence from the more species rich central California coast, or the southern end where the Oregonian and Californian biogeographic provinces overlap.

Acknowledgments

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All collections were conducted under the CDFG Scientific Collecting Permit #000032 (issued to L.G. Allen).

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Appendix A. Environmental variable data collected for each pool averaged across sampling dates. Algae, boulders, sand, surfgrass, and cobble/shell hash were estimated percent covers. Mussels and anemones were quantified as either none (0), single (1), few (2), some (3) or many (4). Urchins and sea stars were counted than standardized to pool surface area by calculating densities (individuals/m^2).

Site	Pool	Algae	Boulders	Sand	Surfgrass	Cobble/hash	Mussel	Anemone	Urchin	Sea star
Leo Carrillo	1	5.2	0.0	15.2	0.0	25.0	0	2	0.0	0.0
	2	22.0	0.0	29.0	0.0	34.0	1	1	74.6	10.0
	3	26.0	0.0	4.2	0.0	0.0	2	2	18.6	1.0
	4	15.2	56.0	7.2	0.0	0.0	4	1	120.0	2.4
	5	65.0	0.0	10.0	0.0	0.3	1	4	86.7	21.1
Paradise Cove	1	27.0	3.0	10.0	58.0	0.0	0	1	17.1	9.0
	2	75.6	10.0	10.4	2.4	1.0	0	2	32.0	11.2
	3	54.8	0.0	19.4	13.0	2.0	0	2	0.4	3.5
	4	2.6	0.0	17.0	0.0	1.4	0	2	2.3	1.0
	5	6.4	0.0	23.0	0.0	1.0	3	2	0.0	0.3
Resort Point	1	19.0	6.0	0.0	0.0	4.4	0	1	1.0	0.1
	2	17.0	24.0	0.0	0.0	5.4	0	2	12.5	0.4
	3	6.2	11.0	0.0	0.0	12.0	0	2	53.7	0.8
	4	11.0	0.0	0.0	0.0	4.0	0	2	23.8	0.8
	5	40.0	4.2	0.0	0.0	7.2	0	1	0.4	0.0
White's Point	1	10.0	12.0	0.0	0.0	51.0	0	1	39.8	0.2
	2	23.0	30.0	0.2	0.0	4.0	0	3	13.5	2.3
	3	30.0	13.0	6.0	0.0	37.0	1	2	37.3	0.7
	4	25.0	1.3	0.0	0.0	52.5	0	2	109.9	1.6
Little Corona	1	10.2	3.0	0.0	0.0	3.4	2	1	33.0	0.1
	2	19.0	9.0	0.0	0.0	6.2	1	1	2.9	0.0
	3	62.0	0.0	0.0	0.0	28.0	1	1	0.4	0.1
	4	18.0	10.0	0.0	0.0	7.0	0	2	22.0	0.0
Shaw's Cove	0	5.0	0.0	81.3	0.0	7.5	0	1	0.0	0.8
	1	7.8	0.0	88.8	0.0	2.4	0	1	0.0	0.6
	2	56.0	0.0	0.0	0.0	25.0	2	2	33.7	0.2
	4	8.0	15.0	5.0	0.0	64.0	0	1	8.5	0.0
	5	32.0	0.0	0.0	0.0	64.0	1	2	18.5	0.0

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Camatta Canyon amole *Hooveria purpurea* var. *reducta* (Agavaceae): a Threatened Plant in La Panza Range, San Luis Obispo County, California

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Abstract.—Camatta Canyon amole *Hooveria purpurea* var. *reducta* (Agavaceae) is a bulbous, perennial plant known from four occurrences in La Panza Range and adjacent hills in central San Luis Obispo County, California. The species *H.* [*Chlorogalum*] *purpurea* was listed as threatened under the U.S. Endangered Species Act in 2000. As currently known, Camatta Canyon amole is narrowly distributed, with a geographic range of 3.05 km^2 and area of occupancy >36.47 ha, of which 21.15 ha are on Los Padres National Forest. Based upon preliminary search on a nearby private property, Camatta Canyon amole likely has greater distribution and abundance here than on national forest. Our data suggest the number of plants where monitored on Red Hill Ridge on national forest has declined since the 1980's and 1990's. In 2021, the primary threats are invasive plants, climate change including severe drought and increased temperatures, and road maintenance and vehicles in the right-of-way of St. Hwy. 58. We suspect that targeted cattle grazing, and if not practicable then light cattle grazing, would likely benefit Camatta Canyon amole by reducing invasive plants and thatch. Using all available information and international standards, Camatta Canyon amole in 2021 meets IUCN criteria for the data deficient category, which is due to lack of data for distribution and abundance on private properties.

Camatta Canyon amole *Hooveria purpurea* var. *reducta* (Agavaceae) is a small perennial plant endemic to central San Luis Obispo County, Calif. At Federal listing in 2000, it was known from two occurrences: Red Hill Ridge including Red Hill Mesa on Los Padres National Forest, and 7 km to the south on one private property. Population estimates ranged from 1,000 to 300,000 plants on <4 ha. Primary threats were illegal vehicle trespass on national forest, road maintenance, displacement by invasive annual grasses, and cattle grazing depending upon intensity (U.S. Fish and Wildlife Service [USFWS] 2000). In a 5-year review in 2008 (USFWS 2008), three occurrences were known with population estimates ranging from 100,000 to 500,000 plants on up to 52 ha (Calif. Dept. of Fish and Game 2007; USFWS 2020). Primary threats were cattle grazing on national forest, illegal motorcycle trespass on national forest, displacement by nonnative annual grasses, and wildfire. More recently, Kofron et al. (2013) reviewed the biology and conservation status of Camatta Canyon amole, reporting four occurrences in 2012 with population estimates ranging from 20,000 to 500,000 plants on at least 12 ha.

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They identified the primary threat as invasive plants, and other threats were Botta's pocket gopher *Thomomys bottae*, uncontrolled cattle grazing, road maintenance, and possibly lack of fire. The purpose of the present paper is to expand the knowledge of Camatta Canyon amole, in particular its distribution, ecology, abundance, threats, management and conservation status in 2021. Most importantly, we report the results of our combined data for four separate monitoring studies from 1987 to 2020.

Materials and Methods

Camatta Canyon amole occurs in a semiarid environment with a Mediterranean climate (hot, dry summers; cool, wet winters). Specifically, it occurs in the rain shadow of La Panza Range (northeast side and adjacent hills) in central San Luis Obispo County, mostly on Los Padres National Forest (Kofron et al. 2013). Black Mountain rises to 1,104 m at 6.27 km west of Red Hill Ridge, which is bisected part of its length by Red Hill Rd. (formerly known as Navajo Rd., and Forest Rd. 29S15). Mean annual rainfall in the area is 254 to 356 mm (Natural Resources Conservation Service 2003), falling primarily from October to April.[1]

We studied Camatta Canyon amole from 1987 to 2020, and our efforts included searching for new locations, mapping known occurrences, monitoring and censusing. We combined the data from our four separate monitoring studies on Red Hill Ridge, which was counting the numbers of emergent Camatta Canyon amole in plots during the typical flowering months of April or May. Regrettably the data cannot be tested statistically because of different methods and small sample sizes. In 1987 we established 10 randomly-located, circular plots (each 1.13 m diameter = 1 m^2) on Red Hill Ridge (five plots each side of Red Hill Rd.), which comprised the known extent of the taxon in 1987, and then counted the numbers of emergent Camatta Canyon amole per plot in 1987 and 1988. In 1991 we established 11 new circular plots (each 0.5 m^2) at random along two transects in typical habitat west of Red Hill Rd., and then counted the numbers of emergent plants per plot in 1991, 1992, 1993, 1995, 1996 and 1997. Cattle grazing occurred on Red Hill Ridge during 1987 to 1997 (excluding 1990, USFWS 2020), although we have no precise details. In 2012 we sampled 18 randomly-located, rectangular plots (each 50 m × 0.5 m with counts of emergent plants per 1 m segment) in what appeared to be the densest areas (12 plots east of Red Hill Rd., 6 plots west of it). In 2013 we attempted to find our 10 plots from 1987/1988 by searching for the center pins with a metal detector. We found only the center pin for plot 5, which had been reestablished in 1988 due to vandalism of the pin placed in 1987. Therefore, we reestablished the 10 plots using the stated descriptions of distances from landmarks along with compass bearings (Table 1). In effect, our 10 reestablished plots are in approximate locations in the same immediate vicinities of 1987 rather than precise original locations, including two plots that we shifted slightly due to tree fall or road widening. We counted the numbers of emergent Camatta Canyon amole annually from 2014 to 2020, using the mean number of plants in three adjacent circular plots (OOO; each 1.13 m diameter = 1 m^2 × 3) at each approximate location. The timing of counting was crucial and a source of potential error. Our goal was to count during the time of maximum flowering, but because of travel time and distance to Red Hill Rd., it was often difficult to know and judge the time of maximum flowering. Counting prior to

[1] WorldClimate.com. 2018. La Panza Ranch, San Luis Obispo County, California USA. Available (19 November 2018): http://www.worldclimate.com/cgi-bin/data.pl?ref=N35W120+2200+044767C, 1 p.

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Table 1. Center coordinates and descriptions of 10 circular plots (each = 1 m^2) for Camatta Canyon amole *Hooveria purpurea* var. *reducta* used in 1987 and 1988, and also in 2014, 2015, 2016, 2017, 2018, 2019 and 2020. Plots are on Red Hill Ridge in Los Padres National Forest, central San Luis Obispo County, Calif.

Plot	Center coordinates	Description
1	35.40290/−120.27943	Red Hill Mesa E of Red Hill Rd, 4.3 m N of blue oak, bearing 355°
2	35.40282/−120.27864	Red Hill Mesa E of Red Hill Rd, 6.3 m NW of two small blue oaks (one is dead in 2013), bearing 335°, in line with a dead oak in distance
3	35.40295/−120.27846	Red Hill Mesa E of Red Hill Rd, 26.6 m N of two small blue oaks in plot 2, bearing 22°, in line with an oak in distance.
4	35.40193/−120.28060	Red Hill Mesa W of Red Hill Rd, 10 m W of small blue oak, original bearing 265°, shifted slightly in 2017 due to tree fall, now ~6 m to the N, new bearing 305°
5	35.40279/−120.28022	Red Hill Mesa W of Red Hill Rd, 69.6 m WSW of blue oak in plot 1; 4.7 m SSW of chamise and bearing 205°
6	35.38929/−120.28736	Red Hill Ridge W of Red Hill Rd, 9 m NW of three-trunk blue oak, bearing 320°
7	35.38945/−120.28746	Red Hill Ridge W of Red Hill Rd, 4.6 m NW of two-trunk blue oak, bearing 300°
8	35.40336/−120.27943	Red Hill Mesa E of Red Hill Rd, 3.75 m SE of pipe fence (white paint mark)
9	35.40305/−120.27956	Red Hill Mesa E of Red Hill Rd, 12 m SE of U.S. Forest Service sign
10	35.40331/−120.27970	Red Hill Mesa W of Red Hill Rd, 12 m S of another U.S. Forest Service sign, next to road

or after would produce a low number. For this reason, we do not use our data for 1994 (0.8 plants/m^2 on 26 May), which was obtained late in the flowering season and is an especially low number. Cattle grazing did not occur on Red Hill Ridge during 2012 to 2020. When initiating each of our four monitoring studies, we believed our plots to be a representative sample of a very small geographic range. However, we now know the geographic range and area of occupancy (area within geographic range occupied by the taxon) are likely substantially larger, with most on private property not yet surveyed (USFWS 2020). Using our collective knowledge and experiences, we identified the threats to Camatta Canyon amole and estimated the relative importance of each.

We considered unpublished reports and other documents in files of USFWS, information in the Calif. Natural Diversity Database (CDFW 2020), personal communications with other knowledgeable persons, and the sparse published literature. Using all available information, we summarize the body of knowledge of Camatta Canyon amole, including its taxonomic history, morphological characteristics, phenology, soil type and plant associates, geographic range and distribution, densities and abundance, threats, and conservation measures. We consider a location with the taxon as a separate occurrence if >0.4 km from the nearest occurrence (CDFG 2011). We determined latitude/longitude and elevation with a global positioning system device in the field or with Google Earth aerial imagery and tools. Rainfall data are for Salinas Dam (west of La Panza Range, 21 km southwest of Red Hill Ridge), San Luis Obispo County, which is the nearest weather station with continuous data from 1986 to 2020.[2] Therefore, the rainfall data should be viewed with caution. Latin and common names of plants follow Baldwin et al. (2012) unless otherwise indicated. Photos are by the authors except where credited. In Appendix 1, we discuss each occurrence according to its assigned number in the Calif. Natural Diversity Database (CDFW 2020).

[2] NOAA National Centers for Environmental Information. 2020. Climate data online: record of climatological observations, Salinas Dam (daily summaries). Available (26 August 2020): https://www.ncdc.noaa.gov/cdo-web/search, 404 pp.

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Results and Discussion

Purple amole *Chlorogalum purpureum* was described by Brandegee (1893) from specimens collected in the Santa Lucia Mountains in Monterey County, Calif. Hoover (1964) recognized two varieties: Santa Lucia purple amole *C. purpureum* var. *purpureum*, and Camatta Canyon amole *C. purpureum* var. *reductum*. He diagnosed *C. purpureum* var. *reductum* from the nominate variety by its smaller size, and referred to it as the "dwarf variety:" *C. purpureum* var. *reductum*, 10 to 20 cm tall; and *C. p.* var. *purpureum*, 25 to 40 cm tall (Jernstedt 2012). Recently, Taylor and Keil (2018) separated *C. purpureum* and *C. parviflorum* out of *Chlorogalum* and recognized the new genus *Hooveria* with *H. purpurea* and *H. parviflora*. The latter two species are distinguished from those remaining in *Chlorogalum* by diurnal opening of flowers, small flowers with styles longer than the perianths, and $2n = 60$ chromosomes (in *H. parviflora* and *H. p.* var. *purpurea,* unknown in *H. purpurea* var. *reducta*), along with significant molecular differences that support this arrangement in Agavaceae (Halpin and Fishbein 2013; Archibald et al. 2015). *Hooveria purpurea* var. *reducta* has the same morphological characteristics and geographic distribution as the previously recognized *C. purpureum* var. *reductum*, and it is the same listed entity. The scientific name *Hooveria purpurea* var. *reducta* is in honor of Dr. Robert F. Hoover (1913–1970), an eminent Calif. botanist, and to its purplish flowers and diminutive stature (Fig. 1). The common name Camatta Canyon amole is in reference to a paratype locality for "upper Camatta Canyon" (Hoover 1964).

Hooveria purpurea is endemic to Monterey and San Luis Obispo Counties in central coastal Calif., and it was listed as threatened in 2000 under the U.S. Endangered Species Act (USFWS 2000). *Hooveria purpurea* var. *reducta* was previously listed as rare in 1978 under the Calif. Endangered Species Act (CDFW 2016), and both varieties are recognized also as 1B.1 rare plants (seriously threatened) by the Calif. Native Plant Society (CDFW 2019). *Hooveria p.* var. *purpurea* is known from 17 occurrences in the Santa Lucia Range in southwestern Monterey County (Fort Hurter Liggett) and north central San Luis Obispo County (Camp Roberts). *Hooveria purpurea* var. *reducta* is currently known from four occurrences in La Panza Range and adjacent hills in central San Luis Obispo County (Fig. 2), mostly on Los Padres National Forest but likely with substantially greater area of occupancy on nearby private property not yet surveyed (USFWS 2020).

Hooveria purpurea is a bulbous, perennial plant. Bulbs are 2.5 to 3.0 cm long, white to brown in color, and those of *H. purpurea* var. *reducta* are situated 5.0 to 6.5 cm beneath the soil surface. A basal rosette of green leaves (up to ~14 in number) develops during the wet season (Fig. 3). Leaves are linear blades with wavy margins, 2 to 5 mm wide. Flowers are deep blue to purple with yellow anthers, open diurnally, and are positioned on multiple branches arising from a single stem. Fruits are capsules with three valves containing one or two black seeds (USFWS 2002, 2020; Jernstedt 2012; Taylor and Keil 2018).

Camatta Canyon amole produce flowers and fruits for just a few weeks from mid-April to late June, most likely dependent on rainfall, sunlight and temperature. Early records of flowering are 14 April 2013 and 18 April 1990 (USFWS 2020). A very late record is 26 June 1998,[3] with a report of 100% of plants along Red Hill Rd. having flowers and 25% of these with fruit. The year 2018 was a poor year for Camatta Canyon amole. Although we recorded a mean of 3.6 plants/m^2 in 10 plots along Red Hill Rd. on 25 April 2018,

[3] Bainbridge, S. 1998. Calif. native species field survey form for *Chlorogalum purpureum* var. *reductum*, 26 June 1998. Submitted to Calif. Dept. of Fish and Game, Sacramento, 2 pp.

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Fig. 1. Upper: Camatta Canyon amole *Hooveria purpurea* var. *reducta* (Agavaceae) on Red Hill Ridge in Los Padres National Forest, central San Luis Obispo County, Calif., 23 April 2019. Lower: Camatta Canyon amole on Red Hill Ridge, 14 April 2013. Photo credit Christopher J. Winchell.

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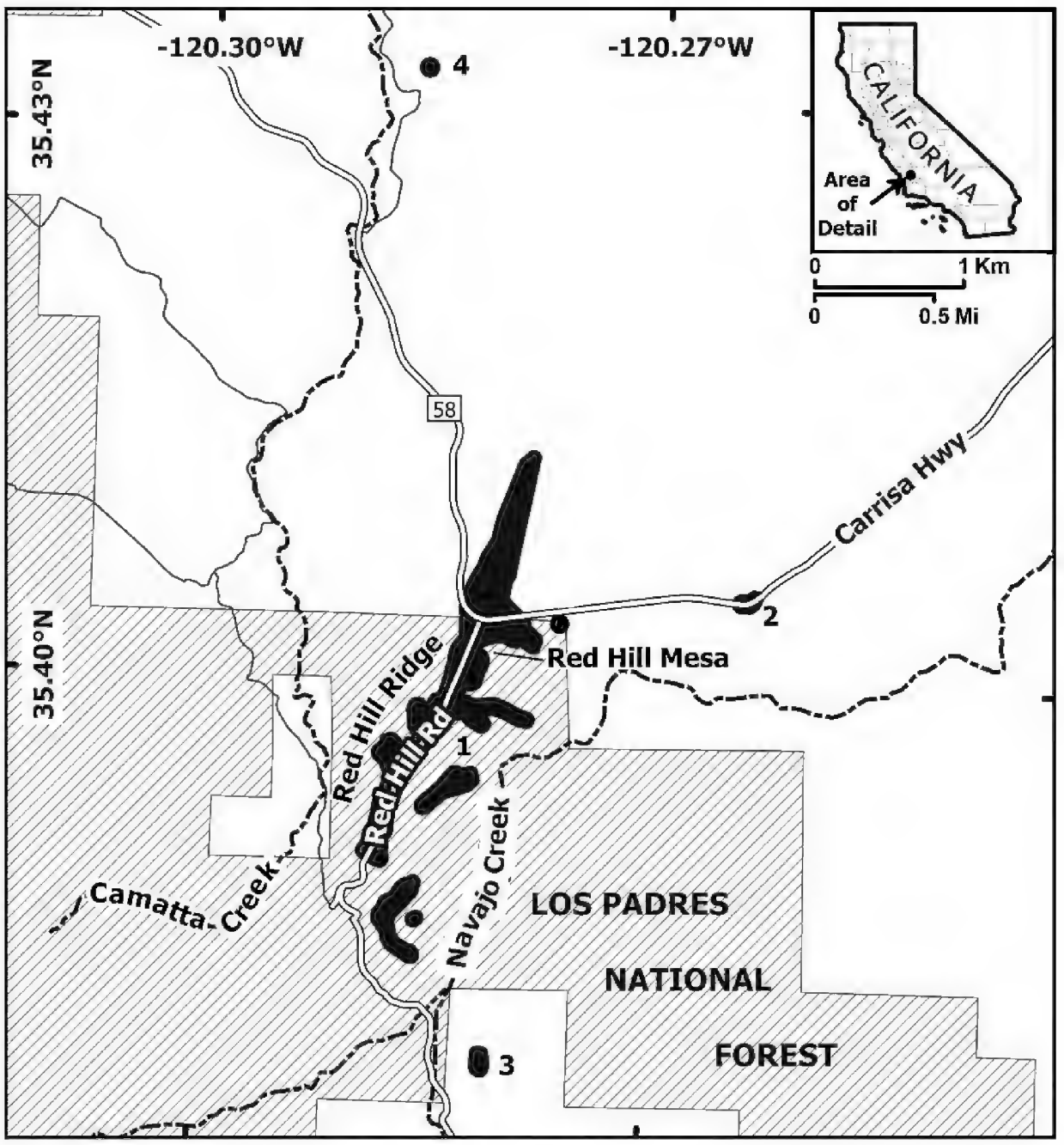

Fig. 2. Geographic distribution of the four known occurrences of Camatta Canyon amole *Hooveria purpurea* var. *reducta* in central San Luis Obispo County, Calif. Each occurrence is indicated by its respective number in the Calif. Natural Diversity Database.

most plants were wilted or wilting, and only a few had flower stems and buds but no flowers. Thus, it appears most plants did not attain the flowering stage in 2018. Regarding the fewer plants that were still green, the leaves had been eaten on most. We speculate that environmental conditions were sufficient to start the process leading to flowers and fruits, but not sufficient to conclude. Normally as fruits mature, the leaves wither, and the inflorescences dry and turn brown. Seeds of Camatta Canyon amole planted on Red Hill Ridge required at least 12 yr to produce flowers and seeds (Koch and Hillyard 2009). Plants are dormant as underground bulbs during summer and fall, and bulbs can likely remain dormant for multiple years like *H. p.* var. *purpurea* (Kofron et al. 2013; USFWS 2020).

Camatta Canyon amole grow in hard, rocky red soil (mapped mostly as Arbuckle sandy loam, Natural Resources Conservation Service 2003; Fig. 3)[4] in relatively flat and level

[4]Natural Resources Conservation Service. 2018. Web soil survey: area of interest, Red Hill Road, San Luis Obispo County, Calif. Available (27 November 2018): http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx.

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Fig. 3. Upper: Camatta Canyon amole *Hooveria purpurea* var. *reducta* (Agavaceae) with well-developed basal rosette on Red Hill Mesa in Los Padres National Forest, central San Luis Obispo County, Calif., 24 March 2010. Photo credit David J. Keil. Lower: Four Camatta Canyon amole with biological soil crust (black material) on Red Hill Mesa, 18 April 2017. Leaves and stems (of three plants) have been eaten by an unknown herbivore.

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Fig. 4. Habitat of Camatta Canyon amole *Hooveria purpurea* var. *reducta* along the top of a spur ridge, east of Red Hill Ridge in Los Padres National Forest, central San Luis Obispo County, Calif., 18 April 2017. Key habitat characteristics are relatively flat and level open areas, and hard, rocky red soil (mapped as Arbuckle sandy loam).

open areas away from trees and shrubs with a light cover of native plants in blue oak (*Quercus douglassi*) savanna, blue oak woodland and Calif. prairie (Fig. 4). In addition, we suspect Camatta Canyon amole inhabits soil that has never been turned for cultivation, like Santa Lucia purple amole (Kofron et al. 2013). Plants often grow with biological soil crusts (cyanobacteria, lichen and moss on the soil surface; Fig. 3), which are important elements of arid and semiarid ecosystems (Beymer and Klopatek 1992). Biological soil crusts stabilize soil against erosion, fix atmospheric nitrogen, form organic matter (Eldridge and Greene 1994), retain soil moisture, discourage weed growth (Belnap et al. 2001), and provide favorable sites for growth of native plants (Lesica and Shelly 1992). Native plant associates include blue oak, chamise *Adenostoma fasciculatum*, crown brodiaea *Brodiaea coronaria*, winecup clarkia *Clarkia purpurea*, sand pygmyweed *Crassula erecta*, blue dicks *Dipterostemon capitatus*, sanicle *Sanicula* sp., Calif. goldfields *Lasthenia californica*, sky lupine *Lupinus nanus*, and gilia *Gilia* sp. (USFWS 2002; pers. obs.).

Camatta Canyon amole is considered most abundant on Red Hill Mesa (Kofron et al. 2013), which is a plateau south of St. Hwy. 58 with eroded slopes on both sides to the east and west. Its vegetation is mostly blue oak savanna, and with chamise chaparral and blue oak woodland on the slopes (U.S. Forest Service [USFS] 2005). It is an alluvial terrace with soil (mapped as Arbuckle sandy loam, slope <10%) having an iron-enriched sandy matrix dominated by gravel and derived from sandstone and shale. In vicinity of Red Hill Rd., Arbuckle sandy loam has a greater mapped distribution north of St. Hwy. 58 than south of

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Table 2. The four known occurrences of Camatta Canyon amole *Hooveria purpurea* var. *reducta* in central San Luis Obispo County, Calif. Measurements of known areas of occupancy exclude Red Hill Rd. and St. Hwy. 58.

Occurrence		Known area of occupancy	Protected	Land use	Year last observed
1	private property N St Hwy 58	>14.84 ha	no	primarily cattle ranching[A] potentially farming[B]	2019
	right-of-way St Hwy 58	313 m^2	no	roadside	2020
	Los Padres National Forest	21.15 ha	yes	multipurpose	2020
2	right-of-way St Hwy 58	882 m^2	no	roadside	2020
3	private property S St Hwy 58	0.36 ha	no	rural residential	2015
4	private property N St Hwy 58	unknown	no	rural residential cattle ranching[A] potentially farming[B]	1988

[A] including non-targeted cattle grazing and exotic wildlife.
[B] dry farming for barley and wheat previously occurred over a large area of the property.

it (Natural Resources Conservation Service 2003; USFWS 2011, 2020).[4] In consideration of mapped soil and similar landscapes, Camatta Canyon amole has potential for a greater occupied area on private property north of St. Hwy. 58 than on national forest. USFWS (2002) designated critical habitat for Camatta Canyon amole over 1,324 ha of private land, and most of it north of St. Hwy. 58. According to Natural Resources Conservation Service (2003), Arbuckle sandy loam with slope <10% comprises 1,066 ha in this area.

As currently known, Camatta Canyon amole is endemic to La Panza Range and vicinity in central San Luis Obispo County, occurring in the rain shadow at intermediate elevations (488 to 633 m) on the northeast side and adjacent hills. Four occurrences are recognized on four properties (Table 2), 61 km southeast of the nearest occurrence of the nominate variety on Camp Roberts. The plant appears to be narrowly distributed but likely has greater distribution. Learning the full distribution is hindered by its short time above ground with flowers and lack of access to private properties for searching.

The primary occupied area is occurrence 1 (>36.02 ha, 584 to 633 m elevation) in vicinity of Red Hill Rd. at St. Hwy. 58. Red Hill Rd. is a graded dirt road originating at and south of St. Hwy. 58, which is a two-lane paved road. Red Hill Rd. bisects Red Hill Ridge and Red Hill Mesa for 1.76 km through occurrence 1. The occurrence comprises predominantly Red Hill Ridge (including Red Hill Mesa), which is the main ridge extending south and north (2.9 km), along with four spur ridges and a nearby ridge to the south. All of these have hard, rocky red soil, and Camatta Canyon amole grows in the relatively flat and level open areas. The southernmost one-fifth of Red Hill Ridge overlooks upper Camatta Canyon with Camatta Creek ~390 m to the west.

Also as currently known, Camatta Canyon amole occurs mostly on Los Padres National Forest (21.15 ha; Fig. 2), extending onto both sides of St. Hwy. 58 in the right-of-way (1.2 m beyond each shoulder; 0.12 ha), north onto one private property (>14.84 ha) and also likely east, and 3 km south of St. Hwy. 58 on one private property (0.36 ha). Information is limited for Camatta Canyon amole on the private property north of St. Hwy. 58. Gaskin (USFWS 2020) mapped the taxon on the flat top of Red Hill Ridge extending north of the

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highway (14.84 ha), commenting it grew also in the dirt road where disturbed by scraping, which is contrary to our understanding. In May 2011, Kofron et al. (2013) observed Camatta Canyon amole on this private property from across the boundary fence near Red Hill Rd., counting ~60 plants from one vantage point and also observing predominantly tall grasses with an absence of grazing. According to Yost (USFWS 2020) who visited the property in 2019, the plant likely has greater distribution and abundance here than on national forest. This property is primarily a cattle ranch (129.5 km^2; USFWS 2020). The right-of-way of St. Hwy. 58 is managed by Calif. Dept. of Transport., which designated the relevant area as a Botanical Management Area. This agency monitors irregularly and aims for greater environmental review when planning work here. However, this failed in October 2020 when a work crew without internal coordination cleared a 270 m length of right-of-way with chamise, extending 22 m (167 m^2) into occurrence 2. In the right-of-way, Camatta Canyon amole typically grows away from dense grasses, either among low-growing plants or in open areas around chamise (USFWS 2020). The private property with Camatta Canyon amole south of St. Hwy. 58 is rural residential (4.19 ha), and here it grows in and along a dirt road on a hilltop. The extent of the plant across national forest and private properties is not fully known.

USFWS (2000, 2002) estimated the known area of occupancy to be 5.1 ha: national forest, 3 ha; private property north of St. Hwy. 58, 2 ha; and private property south of St. Hwy. 58, 0.1 ha. The Calif. Dept. of Fish and Game (2007) estimated the area of occupancy (known and unknown) to be 52 ha. Kofron et al. (2013) reported the known area of occupancy to be 12 ha, and with potential for a greater area on private property north of St. Hwy. 58, especially in critical habitat (USFWS 2002). In 2021, the known area of occupancy is >36.47 ha. The geographic range is small, comprising 3.05 km^2 with mostly similar landscape throughout, and spanning 6.75 km from north to south and 1.95 km at broadest width. The extreme points are north 35.436999/−120.284531, south 35.376377/−120.278510, east 35.405449/−120.259102, and west 35.389462/−120.287597. Although information is lacking regarding genetics, we consider the four occurrences to be one geographic population and therefore one genetic population. The historical geographic range and distribution of Camatta Canyon amole appear to be the same as current. We are not aware of any extirpated location or contraction in the geographic range. Thus, the genetic diversity and spatial extent have not likely declined. The two greatest losses of occupied habitat were by construction of St. Hwy. 58 in vicinity of Red Hill Rd. (12.2 m wide × 1.99 km long = 2.43 ha), and by grading of Red Hill Rd. on Red Hill Ridge (10 m wide × 1.76 km long = 1.76 ha).

The greatest estimated numbers of Camatta Canyon amole for each occurrence are the following (USFWS): occurrence 1 – 500,000 plants in 1991;[5] occurrence 2 – 426 plants in 2017; occurrence 3 – several hundred plants in 1997; and occurrence 4 – no estimate. In addition, Gaskin (USFWS 2020) estimated 1,001 to 10,000 plants in 1990 in his mapped area (14.84 ha, part of occurrence 1) of Red Hill Ridge on the private property north of St. Hwy. 58. Our monitoring data for Camatta Canyon amole on Red Hill Ridge from 1987 to 2020 are shown in Tables 3 and 4. In 1987 and 1988 we observed 6.5 plants/m^2 and 10.7 plants/m^2, respectively. From 1991 to 1997, we observed the following numbers of plants: 1991, 18.0/m^2; 1992, 17.8/m^2; 1993, 16.9/m^2; 1995, 23.5/m^2; 1996, 22.9/m^2;

[5] Warner N. 1991. Calif. native species field survey form for *Chlorogalum purpureum* var. *reductum*, occurrence 1, 26 May 1991. Submitted to Calif. Dept. of Fish and Game, Sacramento, 2 pp.

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Table 3. Monitoring of Camatta Canyon amole *Hooveria purpurea* var. *reducta* on Red Hill Ridge in Los Padres National Forest, central San Luis Obispo County, Calif. (part of occurrence 1). Plants/m^2 = mean number of plants in plots sampled by biologists. Rainfall data (1 December to 15 April) are for Salinas Dam (west of La Panza Range), 21 km southwest of Red Hill Ridge, and should be viewed with caution. Biologists were the following: M. Borchert and L.G. Simpson, USFS; C.P. Kofron and C. Rutherford, USFWS; and D.L. Magney, Calif. Native Plant Society.

Year	Plants/m^2	Rainfall mm	Monitoring date	Plots	Biologist
2020	6.9	406	April 29	10 in approximate locations of 1987	Rutherford + Kofron
2019	4.0	756	April 23	10 in approximate locations of 1987	Rutherford + Kofron
2018	3.4	336	April 25	10 in approximate locations of 1987	Rutherford + Kofron
2017	6.7	749	April 18	10 in approximate locations of 1987	Rutherford + Kofron
2016	6.5	373	April 26	10 in approximate locations of 1987	Rutherford + Kofron
2015	0.3	228	April 27	10 in approximate locations of 1987	Rutherford + Kofron
2014	2.4	229	April 30	10 in approximate locations of 1987	Magney, Rutherford + Kofron
2012	5.3[A]	249	May 2-3	18 randomly-located in densest areas, 50 m × 0.5 m each	Simpson, Rutherford + Kofron
1997	19.6	561	April 18	same 11 of 1991	Borchert
1996	22.9	496	April 24	same 11 of 1991	Borchert
1995	23.5	877	May	same 11 of 1991	Borchert
1993	16.9	782	May 25	same 11 of 1991	Borchert
1992	17.8	547	May 7	same 11 of 1991	Borchert
1991	18.0	451	May 24	11 random along two transects in typical habitat, 0.5 m^2 each	Borchert
1988	10.7	288	May 8	9 in same locations of 1987, 1 approximate	Magney
1987	6.5	232	May 9	10 randomly-located in habitat, 1 m^2 each	Magney

[A] 5.3 +/−2.4, CI = 0.95.

and 1997, 19.6/m^2. Cattle grazing occurred on Red Hill Ridge during these two studies, 1987 to 1997. In 2012 we observed 5.3 plants/m^2 (+/−2.4, CI = 0.95). From 2014 to 2020 we observed the following numbers of plants: 2014, 2.4/m^2; 2015, 0.3/m^2; 2016, 6.5/m^2; 2017, 6.7/m^2; 2018, 3.4/m^2; 2019, 4.0/m^2; and 2020, 6.9/m^2. Cattle grazing did not occur on Red Hill Ridge during these two studies, 2012 to 2020. Although the data cannot be tested statistically because of different methods and small sample sizes, we can make two general observations. (1) Substantially more emergent Camatta Canyon amole were observed in our plots from 1987 to 1997 (8 yr, range of means 6.5 to 23.5/m^2,

Table 4. Numbers of emergent Camatta Canyon amole *Hooveria purpurea* var. *reducta* observed in 10 plots during 9 years from 1987 to 2020 on Red Hill Ridge in Los Padres National Forest (part of occurrence 1), central San Luis Obispo County, Calif. Each plot was in approximate same location from year to year. Plots shaded in gray (1, 2, 3, 4, 9 and 10) show obvious decline in numbers of plants since 1987 and 1988.

	Plot											
Year	1	2	3	4	5	6	7	8	9	10	Total	Mean
2020	0.0	0.0	0.0	0.0	17.7	13.3	27.7	9.7	0.7	0.3	69.4	6.9
2019	0.0	0.0	0.0	0.0	12.0	2.3	17.7	8.3	0.0	0.0	40.3	4.0
2018	0.0	0.0	0.0	0.0	10.0	8.3	14.3	0.3	0.7	0.0	33.6	3.4
2017	0.0	0.3	0.7	0.0	16.7	11.0	32.3	5.7	0.0	0.0	66.7	6.7
2016	0.0	0.0	3.3	0.0	18.3	13.3	24.0	5.0	0.7	0.0	64.6	6.5
2015	0.0	0.0	0.0	0.0	0.7	1.3	0.7	0.3	0.0	0.0	3.0	0.3
2014	0.0	0.0	1.0	0.0	4.3	2.0	13.3	1.0	1.3	1.0	23.9	2.4
1988	4	7	15	8	16	13	14	6	13	11	107	10.7
1987	4	3	8	4	9	9	7	5	9	7	65	6.5

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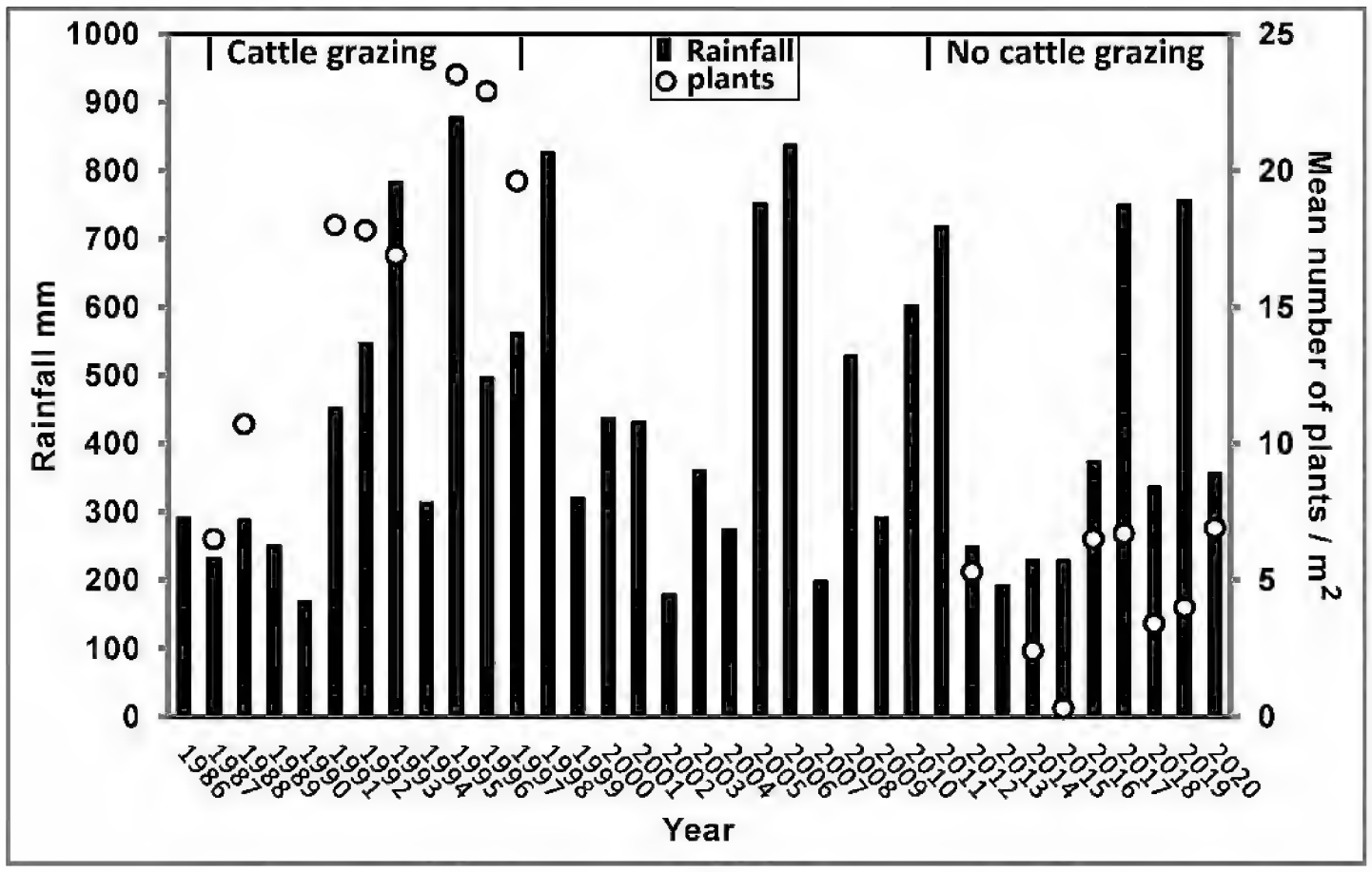

Fig. 5. Mean numbers of emergent Camatta Canyon amole *Hooveria purpurea* var. *reducta* in plots on Red Hill Ridge in Los Padres National Forest, central San Luis Obispo County, Calif. (part of occurrence 1). Monitoring was conducted by biologists identified in Table 3, and it did not occur every year. Rainfall data (1 December to 15 April) are for Salinas Dam (west of La Panza Range), 21 km southwest of Red Hill Ridge, and should be viewed with caution. Precise details of cattle grazing on Red Hill Ridge from 1987 to 1997 are not known. The data cannot be tested statistically because of different methods and small sample sizes.

mean 17.0/m^2), which corresponded in time to cattle grazing, than from 2012 to 2020 (8 yr, range of means 0.3 to 6.9/m^2, mean 4.4/m^2; Fig. 5), which corresponded in time to no cattle grazing. (2) None of the 20 original plots in 1987 and 1988 had 0 plants/m^2, whereas 32 of 70 reestablished plots (46%) from 2014 to 2020 had 0 plants/m^2. Therefore, the combined data of the four studies suggest the number of Camatta Canyon amole where monitored on Red Hill Ridge has declined since the 1980's and 1990's.

In 2021, the primary threats to Camatta Canyon amole are invasive plants (Table 5), climate change including severe drought and increased temperatures, and road maintenance

Table 5. Identified threats to Camatta Canyon amole *Hooveria purpurea* var. *reducta* in 2021: primary, secondary, minor, and potential. Climate change includes severe drought and increased temperatures.

Occurrence	Invasive plants	Climate change	Gophers	Off-highway vehicles	Road vehicles	Road maintenance	Heavy cattle grazing	Farming
1 -private property N St Hwy 58	primary	primary				potential	potential	potential[A]
-right-of-way St Hwy 58	primary	primary			primary	primary		
-Los Padres National Forest	primary	primary	secondary	secondary	minor	minor	potential	
2 right-of-way St Hwy 58	primary	primary			primary	primary		
3 private property S St Hwy 58	primary	primary			minor	potential		
4 private property N St Hwy 58	primary	primary					potential	potential[A]

[A] Dry farming for barley and wheat previously occurred over a large area of the property.

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Fig. 6. Upper: Tall invasive grass (up to 55 cm, slender wild oat *Avena barbata*) in habitat of Camatta Canyon amole *Hooveria purpurea* var. *reducta* on Red Hill Mesa in Los Padres National Forest, central San Luis Obispo County, Calif., 26 April 2016. White circle denotes plot 2 (1987,1988, 2014, 2015, 2016, 2017, 2018, 2019, 2020). Numbers of emergent Camatta Canyon amole in the plot have declined since the 1980's: 1987–3, 1988–7, 2014–0.0, 2015–0.0, 2016–0.0, 2017–0.3, 2018–0.0, 2019–0.0, and 2020–0.0. Lower. Welded pipe fence along Red Hill Rd. on Red Hill Mesa that prevents off-highway vehicles entering habitat of Camatta Canyon amole, 18 April 2017. C. Rutherford's (USFWS, Ventura, Calif.) outstretched hand is above plot 10 (1987,1988, 2014, 2015, 2016, 2017, 2018, 2019, and 2020). Numbers of emergent Camatta Canyon amole in the plot have declined since the 1980's: 1987–7, 1988–11, 2014–1.0, 2015–0.0, 2016–0.0, 2017–0.0, 2018–0.0, 2019–0.0, and 2020–0.3.

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and vehicles in the right-of-way of St. Hwy. 58 (occurrences 1 and 2). Secondary threats are gophers on Los Padres National Forest, and off-highway vehicles along the Burnout Trail on national forest (USFWS 2020). Minor threats are vehicles and road maintenance along Red Hill Rd. Potential threats are heavy cattle grazing, farming, and road maintenance on the private property north of St. Hwy 58 (occurrence 1) and on the private property south of it (occurrence 3). However, targeted cattle grazing (adding and removing cattle on demand to control density and timing at a particular location), and if not practicable then light cattle grazing, may be beneficial. A possible threat may be lack of fire in its habitat on national forest.

The predominant invasive species in habitat of Camatta Canyon amole on Red Hill Ridge are slender wild oat *Avena barbata*, red brome *Bromus rubens*, soft chess *B. hordeaceus* and storksbill *Erodium* sp. The precise effect of invasive species on Camatta Canyon amole is not known, however, they are likely competitors for nutrients and moisture in the harsh environment, and also for sunlight. In addition, they cause accumulation of thatch that can result in exclusion of native plants (Molinari and D'Antonio 2020). In contrast, Camatta Canyon amole favors a bare soil surface and often with biological crust. Much of Red Hill Mesa is now covered with invasive grasses (Fig. 6), which in 2017 were up to 76 cm tall. Camatta Canyon amole is usually absent in tall or dense invasive grasses, except at the southern end of Red Hill Ridge where it grows with dense *Festuca* sp. up to 25 cm tall (Fig. 7; see plots 6 and 7, Table 4). In May 2011, Kofron et al. (2013) reported Camatta Canyon amole generally absent among taller invasive plants (30 to 46 cm) that were especially dense around blue oaks. In contrast, a previous staging area for off-highway vehicles with relatively few invasive plants contained 3.2 Camatta Canyon amole/m^2. Hoover (1970) reported Camatta Canyon amole growing around oak trees on Red Hill Ridge were taller, which he presumed due to looser soil and more humus. However, we observed a general absence of Camatta Canyon amole beneath oak trees. We often encountered individuals at the margins of small grass islands, but not where grass height exceeded 10 cm and 79% cover, such as beneath blue oaks and in the center of grass patches. We usually observed tall and dense invasive grasses in the shaded understory (Fig. 7). It may be that ecological conditions have changed on Red Hill Ridge since Hoover (1970) made his observations, with a possible decline in quality of habitat.

Climate change including severe drought and increased temperatures is a primary threat to Camatta Canyon amole. The 3-yr period from 2012 to 2014 was the hottest and driest in Calif. in the 100-yr time frame considered by Mann and Gleick (2015), and it included the most severe drought in Calif. in the past 1,200 yr (Griffin and Anchukaitis 2014). The six consecutive years from 2013 to 2018 are each among the 10 warmest on record, all 10 having occurred since 2005.[6] The most recent 5-yr (2015 to 2019) and 10-yr (2010 to 2019) periods are almost certain to be the warmest on record, and each successive decade since the 1980's has been warmer than any preceding decade since 1850.[7] San Luis Obispo County ranks 11th in the USA (along with Santa Barbara, Kern and Kings Counties) for

[6] NOAA National Centers for Environmental Information. 2019. State of the climate: global climate report – September 2019. 2019 year-to-date temperatures versus previous years. Available (December 2019): https://www.ncdc.noaa.gov/sotc/global/201909/supplemental/page-1.

[7] World Meteorological Organization. 2019. WMO provisional statement on the state of the global climate in 2019. Available (December 2019): https://library.wmo.int/doc_num.php?explnum_id=10108.

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Fig. 7. Upper: Tall invasive grass (slender wild oat *Avena barbata*) in shaded understory of a blue oak on Red Hill Ridge in Los Padres National Forest, central San Luis Obispo County, Calif., 26 April 2016. Invasive grasses are often taller and denser in shaded understories of blue oaks, and where Camatta Canyon amole *Hooveria purpurea* var. *reducta* is usually absent. Plot 7 (1987, 1988, 2014, 2015, 2016, 2017, 2018, 2019, 2020) is in the foreground. Sixteen emergent Camatta Canyon amole are in the white circle (= 1 m^2). Lower: Dense invasive grass (*Festuca* sp., up to 25 cm tall) in habitat of Camatta Canyon amole on Red Hill Ridge, 18 April 2017. White circle denotes plot 7 as indicated above. Numbers of emergent Camatta Canyon amole in the plot have not declined since the 1980's: 1987–7, 1988–14, 2014–13.3, 2015–0.7, 2016–24.0, 2017–32.3, 2018–14.3, 2019–17.7, and 2020–27.7.

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time duration in exceptional drought (the most intense) since 2000,[8] with most of it having occurred between 2011 and 2015. In brief, Calif. is becoming hotter and drier, and Camatta Canyon amole is in an area that modelling forecasts increased temperatures and increased drying (Anacker et al. 2013). The available information suggests that Camatta Canyon amole is moderately to highly vulnerable to climate change including severe drought and increased temperatures.

Gophers are a secondary threat to Camatta Canyon amole, causing extensive disturbance to habitat on Red Hill Ridge, especially where invasive grasses are abundant. Gophers make holes in the flat soil surface and throw soil into mounds (Fig. 8). We have seen only a few Camatta Canyon amole growing in soil turned by gophers, and the disturbed soil appears favored by invasive plants. Kofron et al. (2013) previously reported gophers causing extensive disturbance to the habitat, especially where invasive plants were abundant. They considered it a new threat since listing, first identified by them in 2010. Previously in the 1990's we observed a substantial amount of gopher activity surrounding but not within habitat of Camatta Canyon amole on Red Hill Ridge. However, Koch (USFWS 2020) reported gopher mounds near her study site on Red Hill Ridge in 1997: "nothing growing on them but amole plants. Amole seedlings would also be visible on these disturbed mounds that had less competition from other plants."

The area occupied by Camatta Canyon amole on Los Padres National Forest is in the Pozo-La Panza Unit (70 km^2), which is best known for off-highway vehicle recreation, and Red Hill Rd. at St. Hwy. 58 is a main entrance (USFS 2005). We and Koch (USFWS 2020) recognized off-highway vehicles as a threat in the 1980's and 1990's. Lopez (1992) observed that off-highway vehicles on Red Hill Mesa resulted in major soil compaction and the probable loss of many plants. More recently, Kofron et al. (2013) reported that habitat on Red Hill Ridge was effectively protected from off-highway vehicles by fencing, signs and ranger patrols. In 2021, habitat on Red Hill Ridge appears to be effectively protected from off-highway vehicles, especially by the welded pipe fence installed in 1990/1991 (Fig. 6) and maintained by USFS. However, the southernmost ridge of occurrence 1 is open to motorcycles and all-terrain vehicles (USFWS 2020), which comprises a secondary threat. Specifically, the Burnout Trail extends through two occupied areas on this ridge (pers. obs.; USFWS 2020), and Camatta Canyon amole is immediately next to and away from the trail.

The adverse effects of road maintenance along Red Hill Rd., in particular grading of the dirt road after the wet season, is ongoing. Although some Camatta Canyon amole grow between the road and pipe fence, we consider road maintenance here to be a minor threat. Also relatively minor are effects of road vehicles running over plants in and near the dirt roads (Red Hill Rd., private property south of St. Hwy. 58), and road vehicles throwing up dust that settles on plants along Red Hill Rd. However, road maintenance and vehicles in the right-of-way of St. Hwy. 58 are a primary threat to occurrence 2 because of its small occupied area.

Red Hill Ridge and Red Hill Mesa are in the Camatta Special Interest Area (22 ha), and also in the Navajo Allotment (1103 ha) where a permittee used to graze cattle from February to May (USFS 2005), which overlaps in time with flowering and fruiting of Camatta

[8] Bolinger, B. 2019. How drought prone is your state? A look at the top states and counties in drought over the last two decades. Available (December 2019): https://www.drought.gov/drought/news/201908.

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Fig. 8. Upper: Habitat of Camatta Canyon amole *Hooveria purpurea* var. *reducta* disturbed by Botta's pocket gopher *Thomomys bottae* on Red Hill Mesa in Los Padres National Forest, central San Luis Obispo County, Calif., 2 May 2012. The disturbance favors invasive plants. Camatta Canyon amole requires a relatively flat and level soil surface. Lower: Habitat of Camatta Canyon amole disturbed by cattle grazing on Red Hill Mesa, 1 May 2010. Disturbance occurred when the soil was wet and soft. We suspect that targeted cattle grazing (adding and removing cattle on demand to control density and timing), and if not practicable then light cattle grazing, would likely benefit Camatta Canyon amole by reducing invasive plants and thatch.

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Canyon amole (mid-April to late June). All known areas for the threatened plant on national forest are in this grazing allotment. Lopez (1992) observed that heavy cattle grazing on Red Hill Ridge resulted in major soil compaction and the probable loss of many plants. Based on our observations over the past decade, cattle grazing occurred here in 2010 (Fig. 8) but not 2011 to 2020. Kofron et al. (2013) reported that in 2010 the soil surface was imprinted with hoof depressions from cattle when the soil was wet and soft. In 1983, McLeod (USFWS 2020) stated that light to medium grazing appeared to benefit Camatta Canyon amole on Red Hill Mesa. In the 1980's we considered heavy cattle grazing a likely threat but light cattle grazing an acceptable land use. Kofron et al. (2013) speculated that targeted cattle grazing may benefit Camatta Canyon amole by reducing the presence of invasive plants and thatch.

Cattle can cause physical damage to Camatta Canyon amole by trampling, along with disruptions to the flat soil surface, soil compaction and erosion, damage to biological soil crusts, addition of manure, reduced presence of native plants and increased presence of invasives (Fleischner 1994; DiTomaso 2000; Belnap and Eldridge 2001; Kimball and Schiffman 2003). In central California, Germano et al. (2001, 2012) recommended targeted cattle grazing for reducing invasive grasses and benefiting native plants and wildlife, and Gennet et al. (2017) determined that targeted cattle grazing can reduce thatch and invasive species while benefiting native plants and birds. In consideration of all factors, we suspect that targeted cattle grazing, and if not practicable then light cattle grazing, would likely benefit Camatta Canyon amole by reducing invasive plants and thatch. In particular, we recognize that cattle ranching can benefit listed species, and USFWS previously led efforts to establish the Calif. Rangeland Conservation Coalition (Barry et al. 2007). With more than two-thirds of Calif. in private ownership, the future of the State's native plant and wildlife habitats is largely dependent on the conservation practices of private landowners (USFWS 2019).

The private property north of St. Hwy. 58 is primarily a cattle ranch (USFWS 2020), and Lopez (1992) described the area with Camatta Canyon amole near Red Hill Rd. (USFWS 2020) as heavily grazed. Although the distribution and abundance of Camatta Canyon amole on this private property are not known, the plant likely has greater distribution and abundance here than on national forest (USFWS 2020). However, we have no additional details. A large area of the ranch was previously dry farmed for barley and wheat. While recognizing that cattle ranching along with wildlife habitat may be the best agricultural use of the property, Weitkamp and Graves (1998) suggested that rotation with commercial legumes and grains (including tilling and fertilizing) could improve the soil and increase livestock and grain production. If this farming is conducted in habitat of Camatta Canyon amole, the habitat would be destroyed and the plant eliminated. In brief, dry farming on the private property north of St. Hwy. 58 is a potential threat to Camatta Canyon amole. In addition, road maintenance is a potential threat on the private property north of St. Hwy. 58 (occurrence 1) and on the private property south of it (occurrence 3).

The effect of wildfire on Camatta Canyon amole is not fully known, however, it would cause loss of the seed crop (Kofron et al. 2013), and it seems intense wildfires with greater fuel loads could kill the underground bulbs. A lack of wildfire allows accumulation of thatch and proliferation of potentially competitive species (invasive and native), whereas fire could possibly benefit Camatta Canyon amole by removing thatch and potentially competitive species. Kofron et al. (2013) observed accumulated thatch and potential competition with invasive grasses (e.g., slender wild oat, red brome, soft chess) and possibly chamise. In general but not quantified, we observed fewer Camatta Canyon amole in plots

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with thatch and tall grasses, which were especially abundant near blue oaks likely because of moisture conservation afforded by shade. Kofron et al. (2013) reported one incident of wildfire likely benefiting *H. purpurea* var. *purpurea* on Fort Hunter Liggett, which was a substantial increase in emergent plants the year after fire. A wildfire along Red Hill Ridge in 1980 (Red Fire) burned chamise, but we subsequently observed no Camatta Canyon amole in the burned stands in May 1981. The last wildfire here was in 1996 (Highway 58 Fire; USFWS 2020).

Conservation measures for Camatta Canyon amole on Los Padres National Forest include signs and a welded pipe fence (with maintenance) along Red Hill Rd. to prevent off-highway vehicles entering habitat, and ranger patrols. Also, biologists of USFS irregularly search/survey/monitor/census on national forest. USFWS with its partners (Calif. Dept. of Transport., Calif. Polytech. St. Univ., Bur. of Land Manage., volunteers) has searched/surveyed/monitored/censused on national forest annually from 2010 to 2020. The right-of-way of St. Hwy. 58 is managed by Calif. Dept. of Transport., which designated the area with Camatta Canyon amole as a Botanical Management Area. This agency aims to give greater environmental review when planning work here, and their biologists search/survey/monitor/census irregularly: 2001, 2005 and 2006 – efforts led by Thomas Edell; 2017, 2018 and 2019 – efforts lead by Michaela Robbins; and 2020 and 2021 – efforts led by Barrett Holland. Botanists at Calif. Polytech. St. Univ. are searching/surveying on the private property north of St. Hwy. 58 in 2021, having conducted a preliminary search in 2019.

Conclusions

Camatta Canyon amole is a habitat specialist with a small geographic range as currently known, and its life history traits appear to include low dispersal ability and soil endemism. Our data suggest the number of plants where monitored on Red Hill Ridge (part of occurrence 1 on Los Padres National Forest) has declined since the1980's and 1990's. In 2021, the primary threats are invasive plants, and climate change including severe drought and increased temperatures. Using all available information and international standards, Camatta Canyon amole in 2021 meets IUCN (2012, 2014) criteria for the data deficient category, which is due to lack of data for distribution and abundance on private properties.

We make the following recommendations to help conserve Camatta Canyon amole and its habitat. (1) Surveys should be conducted to determine the full distribution, and in particular on the private property north of St. Hwy. 58 along with abundance, status and threats. (2) Based on preliminary observations in 2019, a conservation easement should be considered for the private property north of St. Highway 58 (USFWS 2020). (3) Research should be conducted to determine the effects of removing invasive plant species and thatch. (4) Habitat should be restored at occurrence 1 on Los Padres National Forest, in particular by reducing invasive plant species and thatch on Red Hill Ridge, along with monitoring. Targeted cattle grazing may be a useful tool, and if not practicable then light cattle grazing. (5) Signs (educational and regulatory) and a welded pipe fence should be installed at relevant locations along the Burnout Trail in national forest to prevent off-highway vehicles entering habitat. (6) Signs (educational and regulatory; USFS) should be improved at the entrance to Red Hill Rd. from St. Hwy. 58. (7) Seeds should be collected for conservation seed banking, and Camatta Canyon amole should be grown in living collections at several botanic gardens. (8) Calif. Dept. of Transport. should implement its management plan for Camatta Canyon amole, and educate its personnel regarding it.

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Appendix 1

The four known occurrences of Camatta Canyon amole *Hooveria purpurea* var. *reducta* in central San Luis Obispo County, Calif.

Occurrence 1. This is the largest occurrence of Camatta Canyon amole (>36.02 ha), with elevations from 584 to 633 m. It occupies the following areas:

- Red Hill Ridge—relatively flat and level open areas of the ridge top from 1.13 km north of St. Hwy. 58 on private property (35.413525/−120.275893; >14.84 ha) to 1.76 km south of St. Hwy. 58 on Los Padres National Forest (35.388873/−120.286331; 15.37 ha) including Red Hill Mesa, for total distance of 2.9 km; one small area in south right-of-way of St. Hwy. 58 centered at 35.404001/−120.280411 (280 m^2); and several small areas in right-of-way of St. Hwy. 58 near Red Hill Rd. (33 m^2); total area >30.2 ha, 584 to 633 m elevation. The stated areas do not include Red Hill Rd. on Red Hill Ridge (10 m wide by 1.76 km long = 1.76 ha) and St. Hwy. 58.
- top of spur ridge east of Red Hill Ridge on national forest from 35.398554/−120.281274 northwest to 35.397641/−120.275781 for distance of 0.51 km (2.17 ha), 595 to 619 m elevation.
- top of another spur ridge east of Red Hill Ridge on national forest from 35.392162/−120.283337 northwest to 35.394308/−120.279801 for distance of 0.40 km (2.00 ha), 597 to 624 m elevation.
- top of a nearby ridge south of Red Hill Ridge on national forest from 35.387622/−120.283833 south to 35.383117/−120.283806 for distance of 0.50 km (2.49 ha) partly along Burnout Trail, 581 to 628 m elevation; and a hilltop 174 m to the east, centered at 35.385386/−120.283641 (191 m^2) along Burnout Trail, 614 m elevation (USFWS 2020).
- top of another spur ridge west of Red Hill Ridge on national forest from 35.393976/−120.285645 to 35.396216/−120.285809 for distance of 0.25 km (0.64 ha), 621 to 627 m elevation.
- top of another spur ridge west of Red Hill Ridge on national forest from 35.398397/−120.283890 to 35.396270/−120.283523 for distance of 0.24 km (0.95 ha), 607 to 620 m elevation.
- and a location 0.6 km east of Red Hill Rd. in south right-of-way of St. Hwy. 58 at 35.404297/−120.272921, 597 m elevation. USFWS (2020) reported 1 plant here in 2005.

Camatta Canyon amole extends further north and west on the private property (129.5 km^2) north of St. Hwy. 58. According to Yost (USFWS 2020) who visited the property and observed Camatta Canyon amole, the plant likely has greater distribution and abundance here than on national forest, but we have no additional details.

Occurrence 2. 35.405102/−120.259602, 572 to 577 m elevation, along St. Hwy. 58, 1.75 km east of Red Hill Rd. at major curve (just before postmile 27.5), two locations in north right-of-way and one location in south right-of way (and just across the north and south boundary fence lines on two private properties). The known occupied area comprises 882 m^2: south of outer curve, 728 m^2; and north of inner curve, 144 m^2 and 10 m^2. The coordinates and areas are from USFWS (2020). The occurrence is on a mesa extending east from Red Hill Ridge, and the soil is mapped as Arbuckle sandy loam with slope <10% (Natural Resources Conservation Service 2003).[4] The occurrence likely extends further north of the curve where the private property is used for cattle ranching. Twenty-two ha of a private property south and east of the curve have been cleared. The following numbers of plants have been reported (USFWS 2020): 2005, 101 plants; 2006, 90 plants; 2017, 426 plants; 2018, 87 plants; 2019, 279 plants; and 2020, 163 plants. This occurrence is 1.15 km east of occurrence 1.

Occurrence 3. 35.376584/−120.278528, 624 m elevation, on a hilltop on one private property immediately east of Navajo Creek and Red Hill Rd., 3 km south of St. Hwy. 58. This occurrence was first reported in 1997 with an estimate of several hundred plants (USFWS 2020). We visited the occurrence in 2015. During our non-exhaustive search, we observed 15 plants in the hard dirt road on the hilltop, and a few of these may have been on the adjacent property. The known extent of this occurrence is 0.36 ha on one rural residential property (4.19 ha). Based upon similar landscape observed in Google Earth aerial imagery (dated 11 September 2018), the occurrence likely also includes the higher parts of this dissected ridge across multiple private properties from 35.380529/−120.280727 north to 35.369555/−120.275732 south, which spans a distance of 1.21 km. This occurrence is 0.86 km southeast of occurrence 1.

Occurrence 4. 35.436999/−120.284531, 488 m elevation, on a ridgetop, east side of Camatta Creek Rd., 1.2 km north of St. Hwy. 58. This occurrence is based solely on an observation by Clare Hardham in 1988

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(USFWS 2020): "east side of Camatta Creek Rd., about 1 mi north of Hwy. 58, steep hills and a valley, where the cliffs get steep, about 20 yr ago." Using Google Earth aerial imagery (dated 11 September 2018) and Natural Resources Conservation Service (2003),[4] we determine this occurrence is at our stated coordinates, which is mapped as Arbuckle sandy loam with slope <15%. A house occupies the highest part of the ridge at the occurrence. Further, there is evidence of mowing, which likely indicates invasive plants are a threat at this location. We could not gain permission to visit this occurrence on private property (129.5 km^2) that is used primarily for cattle ranching (USFWS 2020). Based upon similar landscape observed in Google Earth aerial imagery, this occurrence likely extends also onto nearby ridgetops to the north, east and west (across Camatta Creek). In addition, unidentified locations and occurrences likely exist further afield in all directions. This occurrence is 2.72 km north of occurrence 1.

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